

Predicting population decline: seagrass demographics and the reconstructive technique

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ABSTRACT: Seagrasses constitute an important component in the nearshore coastal ecosystem, and the declining seagrass habitat is well documented in some areas. A reconstructive technique developed to discern seagrass population demographics with a single sampling event previously predicted the decline of *Thalassia testudinum* populations in Florida Bay, Florida, USA. The results of that model were tested by comparing predicted and actual populations in 1994. A predicted shoot density decline of 49% was not recorded in field populations; instead the population had increased by 51%. We explored 2 potential reasons for the inaccuracy: sampling design, to account for spatial and temporal variability; and data collection procedures that create a demographic bias in the model input. We found that both factors alter the demographic statistics, which modify the model's outcome. Limitations of the model are discussed with respect to its assumptions and interpretation of results.

KEY WORDS: Reconstructive technique · Demography · Population biology · Clonal plant · Seagrass · *Thalassia testudinum* · Florida Bay

INTRODUCTION

Seagrasses are commonly found in shallow littoral zones along temperate and tropical coastlines (Philips & Meñez 1988). In addition to providing habitat and resources to both commercial and non-commercial vertebrates and invertebrates (Orth & Moore 1983), seagrasses filter anthropogenically generated nutrient influx (Dawes 1981) as well as stabilize nearshore sediments (Tomlinson 1974). Declining seagrass coverage was first monitored at the beginning of the 20th century, when the 'wasting disease' devastated seagrass populations in the NW Atlantic (Short et al. 1988). Other marked changes in seagrass coverage have been reported worldwide (Meinesz & Laurent 1978, Kemp et al. 1983, Orth & Moore 1983, Cambridge & McComb 1984, Short et al. 1987, Sanchez Lizaso et al. 1990, Pulich & White 1991) with the implications of habitat loss discussed widely therein.

Historically, seagrass populations have been monitored using yearly changes in seagrass coverage (Robbins & Bell 1994). Recently, seagrass population demo-

graphics, including birth, death and recruitment rates have been used to evaluate potential population decline or increase as an indicator of seagrass health, using an estimate of the plant plastochrone interval (PI) (Duarte et al. 1994). The PI is a measure of the temporal variation associated with biomass production; specifically, it is the amount of time it takes for a plant to repeat an iterated module, such as a leaf (Erickson & Michelini 1957). Calculation of the PI is labor-intensive and requires repeated visits to a site for observations of new growth; in order to reduce the number of site visits to a single trip, a reconstructive technique has been developed for seagrasses (Pergent & Pergent-Martini 1990, Duarte et al. 1994). The reconstructive technique utilizes patterns of leaf scars on the seagrass short shoot as estimators of the PI over time such that a one-time, destructive sampling event can be used to estimate historical seagrass productivity. This technique, if successful, may provide a simple, comprehensive method of evaluating seagrass habitat loss or gain through the generation of a predictive model.

The model utilizes age distributions of living individuals (short shoots), from which recruitment and mortality are calculated. Recruitment is based on an estimate

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of the first year's cohort, and mortality is calculated as the exponential decline in numbers at each age class. Mortality is then used to calculate the population 'half-life', i.e. the postulated time required for half of the population to die off.

In our study, we calculate gross annual shoot recruitment (R_{gross}) for each of 3 stations in Rabbit Key Basin (Florida Bay, FL, USA) and for the Basin (all stations combined), following Duarte et al. (1994), as

$$R_{\text{gross}} = \ln \sum S_{\text{total}} - \ln \sum S_{t+1} \quad (1)$$

where S_{total} represents the total number of shoots and S_{t+1} is the number of shoots older than a year. A year was determined by a PI from Durako (1994), where a new leaf was produced every 18.2 d; by this measure, 20.05 leaf scars indicates a single year's growth.

Mortality (M) is calculated for each station and for the Basin as a whole by fitting a curve through the shoot age data, beginning at the mode of the age distribution (see Fig. 3), using the exponential decay equation

$$M = \frac{-\ln\left(\frac{N_t}{N_0}\right)}{t} \quad (2)$$

where N_t is population size at time t and N_0 is initial population size (Duarte et al. 1994). Mortality estimates are calculated for each station and for the Basin using both attached shoots and total shoot counts.

Differences between gross shoot recruitment (R_{gross}) and mortality (M) estimates are used to predict the increase or decrease of seagrass density with time (R_{net}). Net recruitment for each site, as well as all sites combined (Basin), is calculated as an estimate of population growth or decline using

$$R_{\text{net}} = R_{\text{gross}} - M \quad (3)$$

A negative R_{net} value indicates greater mortality than recruitment, and a declining population. All of the above values (R_{gross} , M and R_{net}) are used as points of comparison between populations. Using the calculated mortality (M ; Eq. 2), future population dynamics have been quantified by projection of the current population's half-life over time, based on the current year's density (cf. Durako 1994). Population half-life ($T_{1/2}$) was calculated by

$$T_{1/2} = \frac{\ln 2}{M} \quad (4)$$

The major assumption of the predictive model employing survival data is a stable age distribution (i.e. constant age-specific mortality and recruitment rates; Krebs 1994). An alternative model for seagrass population dynamics uses age-at-death information (Duarte et al. 1994), but this also necessitates the assumption of a stable population as well as constant birth and death rates within each age group (Krebs 1994).

Using the reconstructive technique on a single sampling event in Florida Bay, Florida, USA, Durako (1994) forecast the population dynamics of the seagrass *Thalassia testudinum*, based on the assumption that mortality and recruitment could be accurately assessed with a one-time sampling. The robustness of the predictive model used by Durako (1994) has not yet been evaluated with regard to sampling strategy or its inherent assumptions. Although variability of demographic characteristics has been assessed for various terrestrial plants, including clonal species (Harper 1977, Birch & Hutchings 1992a, b), demographic characteristics such as fecundity and mortality have not been extensively evaluated for seagrasses, possibly due to the logistical constraints associated with subtidal sampling. Without the knowledge of within-population variability in fecundity and mortality, sampling design becomes increasingly important in the search for a 'representative' population. Another potential bias of the model may be a consequence of sample processing, specifically if the sampling procedure differentially excludes 1 age class. Such may often be the case in seagrass, where older shoots, being longer and more brittle, are more subject to breakage and subsequent exclusion from the data set.

Based on the results and subsequent prediction using a reconstructive model, Durako (1994) suggested a relatively severe seagrass population decline in parts of Florida Bay for the 'near future'. We tested these predictions using data from Durako (1994) along with newly collected information on seagrass shoot dynamics from Florida Bay. Specifically, we examine the variability of demographic characteristics of seagrass among 3 sampling sites within a geographically distinct region, to address 2 questions: (1) do the results of the exponential model's predictions differ as a function of sampling design relative to spatial variability, and/or data collection procedures?; (2) can the reconstructive technique (sensu Duarte et al. 1994) be used to reliably predict seagrass population demographics and dynamics in Rabbit Key Basin?

MATERIALS AND METHODS

Sites. The study was conducted within Rabbit Key Basin, a 52.5 ha, partially enclosed basin located within the southwestern region of Florida Bay, approximately 10 km from the Gulf of Mexico. For a further description of Rabbit Key Basin, see Robblee et al. (1991). Previous work in this area has provided extensive data on the dominant seagrass *Thalassia testudinum* Banks ex König found within the Basin and throughout the Bay (Durako 1994). Three stations (A, B, and C) were haphazardly selected within Rabbit

Key Basin (A: 24° 58.45' N, 80° 50.07' W; B: 24° 57.35' N, 80° 50.07' W; C: 24° 59.91' N, 80° 51.15' W). At each station, an area of 115 m² was haphazardly sampled. Samples were taken at approximately the same depth to minimize variation in growth dynamics due to changing light conditions. There was no attempt to stratify sampling according to seagrass coverage, or to target highly disturbed or recently colonized areas. Data from the 3 stations were used to examine data collection techniques and to compare variability in population demographic characteristics within a region of continuous seagrass cover.

Sampling and analysis. Thirty cores in *Thalassia testudinum* beds were taken at each station using a 15.3 cm diameter PVC corer, to a depth just below the rhizome mat (~30 cm) in approximately 2 m (± 0.5 m) of water. The cores were rinsed free of sediment and all plant material was returned to the laboratory for separation and analysis; care was taken to minimize shoot breakage during rinsing. All samples were collected on 25 June 1994.

To test the model's sensitivity to sampling technique, the fate of shoots during the data collection process was recorded. Shoots were categorized as either 'attached' (still retaining a connection to the rhizome), 'unattached' (broken from rhizome) or 'dead' (the tip broken off and containing black internal tissue). Live versus dead shoots were defined sensu van Tussenbroek (1994), where a green leaf is indicative of a living shoot. All shoots that retained leaves but no horizontal rhizome were considered 'unattached'. The number of leaf scars, plus standing leaves of unattached shoots represent a conservative estimate of the age of the shoot, whether it was broken once (removed from the rhizome) or more than once. The number of leaf scars (LS) plus standing leaves on each shoot (see Fig. 2, Durako 1994), both attached and unattached, were enumerated. Because of the advanced state of decay, no LS counts were taken from dead shoots.

Two age distributions were developed for each station's population, using: (1) attached shoots only and (2) both attached and unattached shoots (total). These data were then pooled to calculate demographic parameters and create age distributions representing the overall Basin population, of both attached and total shoot distributions. Population distributions were smoothed by lumping every 2 age classes (2 PIs). Potential demographic bias attributed to sampling technique was examined by comparing demographic characteristics with 1-way analysis of variance (or Kruskal-Wallis test on ranks when data did not pass normality or equal variance tests) followed by multiple comparison tests where appropriate. Age structures of each site with (total) and without (attached) the addition of broken shoots were compared using a

Kolmogorov-Smirnov 2-sample test. All tests were conducted at a minimum alpha level of 0.05 (Sokal & Rohlf 1981).

To verify the predictive aspect of this model we compared our 1994 shoot densities to predicted 1994 densities using the above equation (Durako 1994). We also compared actual 1994 shoot densities and demographic characteristics to the 1989 and 1990 data in Rabbit Key Basin from Durako (1994).

RESULTS

A total of 1139 'living' shoots was collected and analyzed from the 3 stations. At each station approximately 40% of shoots were found to be unattached. The lowest mean shoot age, in both the attached and total shoot counts, was found at Stn A while the oldest was at Stn C (Fig. 1A). Mean age was significantly different among stations ($p < 0.01$; Table 1), however, Stn A was not significantly different from the mean age of the Basin (Table 1). This pattern was consistent when unattached shoots were included in the analysis

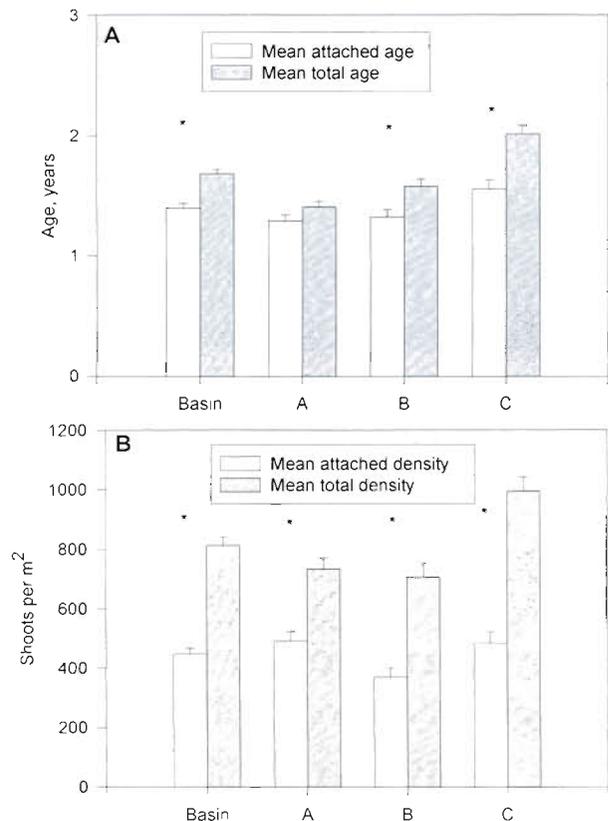


Fig. 1. *Thalassia testudinum* population descriptors: (A) mean (± 1 SE) shoot age; (B) mean (± 1 SE) shoot density. Open bars: attached shoots only; solid bars: attached + unattached shoots. *Significant at $p < 0.05$

Table 1 ANOVA values. A, B and C refer to sampling stations, Basin is all stations combined. Test values: 1: Kruskal-Wallis, followed by Student-Newman-Keuls multiple comparison test, where appropriate; 2: 1-way ANOVA, followed by Student-Newman-Keuls multiple comparison test, where appropriate. ns: non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$

	Test	p	Multiple comparison
Mean shoot age			
Attached shoots	2	*	A B Basin C
Total shoots	2	***	A B Basin C
A attached vs total	2	ns	
B attached vs total	2	*	
C attached vs total	2	***	
Basin attached vs total	2	***	
Shoot density			
Attached shoots	1	ns	
Total shoots	1	***	A B Basin C
A attached vs total	2	***	
B attached vs total	1	***	
C attached vs total	2	***	
Basin attached vs total	2	***	

(Fig. 1A, Table 1). When each station was tested individually, the mean age of only the attached shoots was significantly different from that of the total shoots for all stations except Stn A ($p < 0.01$; Table 1), suggesting that exclusion of unattached shoots decreases the mean age of the sampled population. For example, the age of the oldest shoot at Stn C, when only attached shoots were considered, was nearly twice the age of

Table 2. Demographic characteristics of the 3 sampling stations, and of the whole Basin. Shoots: attached (att) or unattached + attached (tot); n: no. of shoots per core; Max age: age of oldest shoot in population; R_{gross} : gross recruitment in \ln units yr^{-1} ; M : mortality in \ln units yr^{-1} ; R_{net} : net recruitment in \ln units yr^{-1} ; $T_{1/2}$: half-life in yr; nd: no data. See text for calculations

Site	Shoots	n	Max age	R_{gross}	$M (\pm SE)$	R_{net}	$T_{1/2}$
A	att	259	4.2	0.38	0.97 (0.06)	-0.59	0.715
	tot	383	6.5	0.36	0.99 (0.05)	-0.63	0.700
B	att	197	4.1	0.37	0.96 (0.05)	-0.59	0.722
	tot	331	6.4	0.30	0.84 (0.05)	-0.54	0.825
C	att	258	7.9	0.29	1.18 (0.07)	-0.89	0.587
	tot	426	7.9	0.21	0.74 (0.05)	-0.53	0.937
Basin	att	714	7.9	0.34	1.05 (0.03)	-0.71	0.660
	tot	1139	7.9	0.28	0.79 (0.07)	-0.51	0.877
From Durako (1994):							
1989	nd	247	7.6	0.39	0.43	-0.04	1.61
1990	nd	236	5.1	0.55	0.83	-0.28	0.83

the oldest found at either Stns A or B (Table 2). Differences in the age of the oldest shoot when considering all shoots (total) were less distinct among the stations. However, there were both older shoots and greater shoot densities at Stn C than either Stn A or B regardless of whether only attached shoots or total shoots were considered (Fig. 1A).

The density of attached shoots was not significantly different between stations ($p > 0.05$; Fig. 1B, Table 1). When the total shoots (attached + unattached) were examined among stations, the shoot density was significantly higher at Stn C than either Stn A, B or the overall Basin (Table 1). When attached versus total shoots were tested within an individual station, shoot density was found to be significantly different in all stations when unattached shoots were included in the analysis ($p < 0.0001$; Fig. 1B, Table 1).

The average total shoot density of the Basin was 813 shoots m^{-2} . We found that total shoot density in 1994 had not declined as predicted (Durako 1994), but had increased by 51% (Fig. 2). The earlier study suggested a population in decline, with a range of decrease in seagrass shoot density of 15 to 49% yr^{-1} (Fig. 2), based on calculated recruitment and mortality rates (Durako 1994). Because it is not known what proportion of shoots was excluded as a result of breakage in the 1990 study, we also evaluated population density differences using our only attached shoots (Fig. 2). The 1994 densities of attached shoots decreased 15% over the 4 yr interval, rather than 15% yr^{-1} as predicted (Durako 1994).

A comparison of the age distributions of attached shoots among the 3 stations revealed that while Stns A

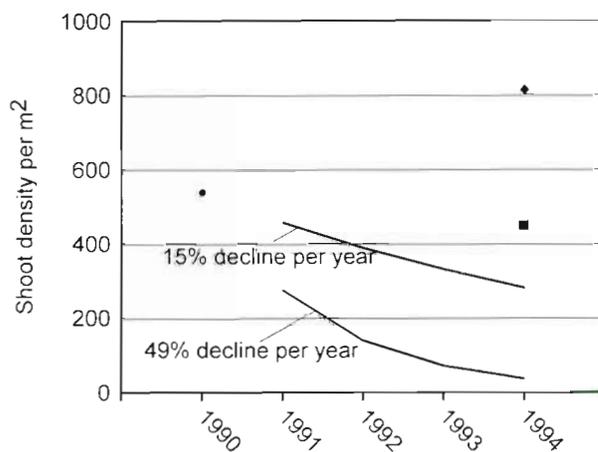


Fig. 2. *Thalassia testudinum*. Test of the model predictions of population dynamics in Rabbit Key Basin, Florida Bay, from Durako (1994). The 15 and 49% lines indicate the range of projected decline across years 1991 to 1994, based on 1990 data. Data from 1994 were from our study, collected in June 1994. (●) 1990 collection; (◆) 1994 collection, total shoots; (■) 1994 collection, attached shoots only

and B were similar (Fig. 3A, B, Table 3), both differed significantly from Stn C (Fig. 3C, Table 3). Only Stn B was similar to the Basin (Fig. 3B, D, Table 3). These differences disappeared with the inclusion of unattached shoots (Table 3). Significant differences between age distributions of only attached and total shoots at Stn C and at the total Basin were found (Table 3). An examination of the Basin's age distribution with all shoots included (total) suggests that any of the 3 stations might be adequate to predict the age distribution for the area as a whole, although this is predicated upon careful sampling (i.e. no data censoring).

Using the formulae outlined by Duarte et al. (1994) and Durako (1994), all R_{net} values were found to be negative (Table 2) suggesting that each station, as well as the Basin, was in severe decline. This pattern was true regardless of whether or not unattached shoots are included in the analysis. Mortality was highest when only attached shoots were included in the distribution (Table 2), except for Stn A. As mortality is calculated by a regression from the highest point on the age distribution curve (modal age), the decrease in mortality when unattached shoots are included reflects the effects of older shoots more likely being detached in the sample processing, thus shortening the tail of the distribution. Population half-life ($T_{1/2}$) increased with the inclusion of unattached shoots at all stations except A (Table 2), again indicating that the unattached shoots tended to be older. The lifespan of the population may be underestimated when unattached shoots are excluded from the analysis.

We compared our demographic parameters of Rabbit Key Basin to those in Durako (1994) (Table 2). Our gross recruitment estimates were 28 and 49% less than those reported for 1989 and 1990, respectively. Mortality and 'half-life' estimates in this study were comparable to those given for 1990, but 200 and 50% respectively of those recorded for 1989 (Table 2). Our net shoot production was less than in either 1989 or 1990 in Durako (1994). In 1994, the Basin value was -0.51 compared to -0.04 and -0.28 for 1989 and 1990 respectively (Table 2). Thus the demographic parameters recorded in 1994 differed markedly from data collected in 1989 or 1990. Overall, our results did not verify the predictive model, whose predictions were based on 1990 data.

DISCUSSION

Our 1994 study on seagrasses in Rabbit Key Basin provides an important perspective on the influence of sampling design and data collection procedures as they relate to the calculation of demographic characteristics of seagrasses. First, of the 3 sample sites exam-

Table 3. Statistical comparisons of age distributions from each sampling station, using the Kolmogorov-Smirnov test of similarity; where $D > D_{max}$, * indicates distributions are significantly different at $p < 0.05$ (Sokal & Rohlf 1981). A, B, C are stations, Basin is all stations combined. att: attached shoots only; tot: attached + unattached shoots

	<i>D</i>	<i>D</i> _{max}
A _{att} vs B _{att}	0.1019	0.0713
A _{att} vs C _{att}	* 0.0956	0.1942
A _{att} vs Basin _{att}	* 0.0802	0.0916
B _{att} vs C _{att}	* 0.0995	0.1420
B _{att} vs Basin _{att}	0.0848	0.0381
C _{att} vs Basin _{att}	* 0.0771	0.1042
A _{tot} vs B _{tot}	0.1284	0.0288
A _{tot} vs C _{tot}	0.1195	0.1048
A _{tot} vs Basin _{tot}	0.0985	0.0444
B _{tot} vs C _{tot}	0.1285	0.0840
B _{tot} vs Basin _{tot}	0.1093	0.0298
C _{tot} vs Basin _{tot}	0.0987	0.0605
A _{att} vs A _{tot}	0.1093	0.0429
B _{att} vs B _{tot}	0.1222	0.0932
C _{att} vs C _{tot}	* 0.1071	0.1489
Basin _{att} vs Basin _{tot}	* 0.0648	0.0895

ined within Rabbit Key Basin, only 2 of the 3 stations provided estimates of seagrass density representative of the total Basin. Only 1 site presented a mean age representative of the Basin, while each site reflected the age distribution of the Basin (Fig. 3, Tables 1 & 3). Secondly, determination of mean shoot age was significantly impacted when data censoring occurred through sample processing. By eliminating unattached shoots from the data analyses, the mean age of the sample population was significantly decreased. These findings warn that collection of information to be used in model construction must be carefully scrutinized for inherent biases which may decrease the accuracy of the predictive model. While addressing biases in sample processing may be relatively straightforward, designing an effective sampling strategy to deal with variation in demographic characteristics is much more problematic. One way to address this is to have adequate preliminary data on spatial and temporal variability of population demographics from the site. However, the necessity of continuous, regular site visits to establish the preliminary information renders the one-time sampling less feasible, especially if the reconstructive technique is to be used at sites that are logistically difficult to access (Duarte et al. 1994). Thus the reconstructive technique may be useful for historical demographic descriptions, but does not appear to be useful as a predictive tool.

The usefulness of a population model for seagrass is predicated upon the ability to estimate population trajectories of increase or decrease. The construction of population demographic characteristics, as presented

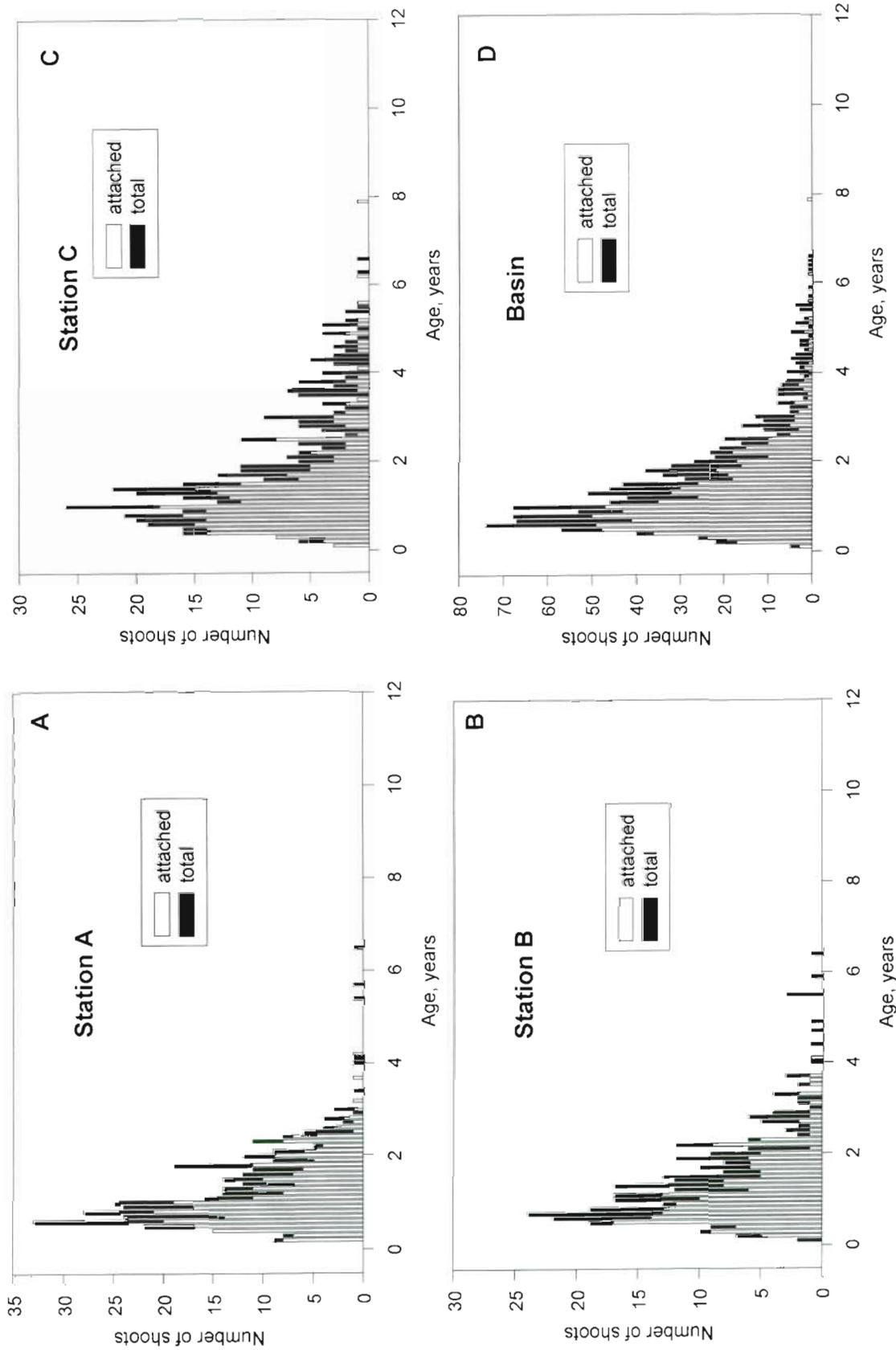


Fig. 3. *Thalassia testudinum*. Age distributions of the populations at 3 sampling stations within Rabbit Key Basin, Florida Bay, for attached and total (attached + unattached) shoots: (A) Stn A; (B) Stn B; (C) Stn C; (D) Basin (= combined data sets of the 3 stations, A, B, C)

by Duarte et al. (1994), may be valid in some seagrass populations, as discussed below; however, a key test of the predictive model's reliability failed at Rabbit Key Basin. This lack of predictive power or accuracy may be the result of problems existing with either the predictive model itself, or with the data used in the model. By tracing the steps involved in the use of the model, and discussing potential sources of error at each step, the usefulness of the model may be most effectively evaluated.

Age distributions and the plastochrone interval

The construction of an age distribution is the first step in the description of a population, whether simply as a descriptor or for use in a population model. Because *Thalassia testudinum* is capable of clonal propagation with indeterminate growth, such that size and age of a shoot are not linearly related, shoot age may be calculated using the plastochrone interval (PI). In many seagrasses, the production of each new leaf is recorded by the presence of a leaf scar on the vertical rhizome (short shoot or ramet). Calculating the PI can be accomplished by repeated observations of the productivity, to establish the number of new leaves that emerge within a given time period (Patriquin 1973). Because distinct annual patterns of leaf scars (LS) are evident in some localities (e.g. Marbá et al. 1994) a less labor-intensive method of calculating the PI has been developed; the number of scars in an annual set is divided by 365 (d yr^{-1}) (lepidochronology; Pergent & Pergent-Martini 1990), translating biological into chronological age (Ritterbusch 1990). In regions where LS annual patterns do not exist or have not been documented, 2 methods may be used to calculate the shoot age. (1) The number of LS per shoot is tallied, a frequency distribution of shoot ages is created (Duarte et al. 1994) and peaks in the distribution are assumed to indicate cohorts. Chronological age is then inferred by further assuming that each cohort represents a single year's reproductive output: if the number of LS between peaks represents the number of leaves produced by that shoot per year, shoot age can then be back-calculated. (2) The long-term leaf-punching techniques of Patriquin (1973) can be used in conjunction with a single sampling event to empirically establish the PI for translating the number of LS to chronological age.

The use of techniques to estimate PI values assumes that the output of new leaves is a continuous, linear process, within some statistically acceptable limits (Brouns 1985). However, because seagrasses undergo seasonal changes in productivity (Romero 1985, Perez et al. 1994), the influence of variation of environmental

conditions such as light or temperature must be considered (Lamoreaux et al. 1978, S. J. Williams, T. Ebert & P. Ewanchuck unpubl.). Small-scale spatial or temporal environmental variability (e.g. light, temperature, wave action) may explain the differences in demographic structure and heterogeneity of the seagrasses at the 3 sampling stations reported here. The contrasting demographic data noted between 1989 and 1990 (Durako 1994) as well as our 1994 data may reflect temporal variability inherent in the population. Conversely, the similarities of some characteristics between 1994 and 1990, but not 1989, indicate that there may be some cyclical population dynamics (C. M. Duarte pers. comm.). However, this would be difficult to discern without a long-term data set. To incorporate the potential temporal variability within the calculated PI, observations should encompass at least several seasons (perhaps over more than 1 yr; Sharpe 1993, Marbá et al. 1994). Where no seasonal patterns exist, or where they have not yet been elucidated, the reconstructive technique may prove fallible and only with repeated observations can there be reliable estimates of the PI (i.e. days elapsed between leaves produced, or days leaf $^{-1}$) (Harper 1977).

Mortality and recruitment

Seagrass recruits to the population have been defined as all shoots less than 1 yr old (Duarte et al. 1994, Durako 1994), where the chronological age is based upon an estimate given by the PI. If sampling is done annually, one might intuitively consider all new shoots produced since the last sampling event to be a recruit. However, the clonal nature of seagrasses may complicate the selection of an age class containing recruits. For example, the mode and the proportion of the population less than a year often overlap (see Fig. 3), such that the same part of the population is included in both mortality and recruitment estimates. The construction of the age distribution is dependent upon the calculation or estimation of the year classes, which is in turn dependent on the calculation or estimation of the PI. While quantitative data are lacking, it has been noted that shoots younger than 1 yr (approximately 20 LS in the Florida Bay samples) are capable of producing lateral meristems, the source of clonal recruits (S. L. Jensen unpubl. data).

The calculation of mortality is dependent upon the ability to distinguish a distinct graphical (i.e. non-statistical) mode in the age distribution. Mortality of a plant population can be calculated in the following ways: by the equation of exponential decay (Eq. 2) starting at the age distribution mode, or via life table calculations using survivorship data. In the series of

equations described above, M is then used to calculate the half-life of the population (or, in effect, the half-death; Durako 1994). The result of that calculation is not how long it will take the population to decline to half of its numbers (indicative of die-off) but rather how long it will take for a cohort to reach the maximum age of death or senescence (dispersion curve rather than a survival curve, Harper 1977). The mortality estimate is calculated from an exponential decay equation and as such the half-life equation, with mortality in the denominator (Durako 1994), will always de facto present a picture of a declining population.

We have shown that the older shoots are more likely to be removed from the analysis through breakage (Figs. 1 & 3, Tables 1–3); this has implications for calculation of mortality. In our study, the inclusion of unattached shoots altered the slope of the curve fit to the age distribution, decreasing M (mortality) and increasing R_{net} (net recruitment). Thus estimates of mortality of the same population might vary simply because the fraction of unattached shoots may be inconsistent between studies, as sample processing may vary among investigators. We hesitate to offer an estimate of the fraction by which the demographic characteristics should be corrected for sampling artifacts.

Use of the age distribution in calculation of mortality and recruitment addresses the issue of the importance of a stable age distribution over time: the modal cohort cannot be determined to be at a particular age class by a single 'snapshot' sampling (Harper 1977). Inspection of figures in Durako (1994) and Olesen & Sand-Jensen (1994) suggests dissimilarities in the age distribution between 2 years. The variability between years may be part of the natural fluctuations of seagrass populations, rather than an indicator of their imminent demise. We suggest that for any prediction of population dynamics, longer-term studies (>2 yr) should be performed, and the attractiveness of a single-sampling effort would no longer be applicable.

The model and its alternatives

The exponential growth equation that has been used in the prediction of future seagrass population size is not commonly used in studies of continuous populations, or involving organisms whose numbers fluctuate widely from season to season, because of the violation of the underlying assumptions: constant r (intrinsic rate of natural increase), stable age distribution and that, over time, birth and death rates are linear, constant and independent of both age and population size (Caughley & Birch 1971, Southwood 1978, Lomnicki 1988, Renshaw 1991). As a descriptor of exponential growth, the model may only be accurate in special

cases of colonization (Pielou 1977, Taylor 1979, Horn 1988), and is unlikely to be applicable as a long-term predictor of established populations because age-dependent survival is often density- and frequency-dependent as well (Lomnicki 1988, Jensen 1995). This may also apply to seagrass populations, where there is an anecdotal correlation of recruitment and mortality (C. M. Duarte pers. comm.).

Use of the reconstructive technique, involving a one-time sampling, cannot measure to what degree the assumptions are violated except in particular cases, e.g. where there are annual patterns of LS, giving an estimate of annual productivity over a time period exceeding 1 yr. When the seagrass system in question does not provide an incontrovertible annual pattern, productivity must be repeatedly measured (Harper 1977). The one-time sampling may provide a biased assessment if taken at a point of seasonal increase or decline in population. Thus the use of a predictive model grounded on a single sampling may not give a reasonable assessment of the population's dynamics. Because the assumptions must be relaxed for use with actual biological populations, the validity of the model is compromised, such that any predictive effects must be limited to very short time periods. It can be argued that biological models with unrealistic simplifying assumptions present null models against which to compare the observed population; difficulty arises when they are used as predictors of future population growth.

Testing the model's assumption of constant mortality and stable age distribution can be accomplished by using life-table calculations of population demographics. Life tables used for estimation of population growth or decline have been used (Olesen & Sand-Jensen 1994), and employ time-step data. Both the assumptions of a stable age distribution and constant mortality are equally difficult to test as they may fluctuate annually. Alternative methods such as age-specific matrix population models (Caswell 1989) have been used extensively for predictions of terrestrial plant population growth, and should be further exploited in calculations of seagrass demography (Williams et al. unpubl.). Unfortunately, these cannot be constructed until more information on individual and population birth and death probabilities has been established (cf. Lomnicki 1988).

CONCLUSIONS

The model currently used to predict seagrass population growth or decline at Rabbit Key Basin was found to be inadequate. Data collected in 1994 do not verify the predictive model, standing in marked contrast to

the earlier predictions, and the assumptions of the model cannot be met or tested. The methods used for data collection may impart a, perhaps correctable, demographic bias. The reconstructive technique for estimation of seagrass demographic characteristics may be used only if there is a temporal component involved in the estimation of the PI; in regions where annual sets of LS are evident, the temporal scale is inherent. Otherwise, repeated sampling must be performed in conjunction with leaf-punching productivity studies over extended time periods, which decreases the attractiveness of a single sampling, quick-and-dirty estimate of seagrass 'health'.

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