Large-scale patterns in seagrass (*Thalassia testudinum*) demographics in south Florida

Bradley J. Peterson[1] *and James W. Fourqurean*
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University,
University Park, Miami, Florida 33199

Abstract

An examination of the population age structure of 118 spatially separated subpopulations of *Thalassia testudinum* over the extent of the Florida Keys National Marine Sanctuary (FKNMS) during a 2-yr period revealed significant spatial variation in short shoot (SS) demographic characteristics and population dynamics. Shoot age was determined for 12,031 SS. The number of leaf scars on individual shoots was converted to shoot age by use of observed seasonally and spatially variable leaf emergence rates. The yearly mean leaf emergence rate was 0.0295 ± 0.0128 leaves SS^{-1} d^{-1} (± 1 SD), and the median age of counted shoots was ~ 5 yr. A significant relationship between asexual reproductive effort and gross recruitment of SS into the populations ($r^2 = 0.15$, $P = 0.001$) and between mortality of SS and gross recruitment ($r^2 = 0.72$, $P < 0.001$) existed. Thus, the greatest risk of mortality occurred in areas where gross recruitment was highest. The net population growth for *T. testudinum* within the boundaries of FKNMS was stable (mean = -0.006 ± 0.089 yr^{-1}). However, areas within FKNMS fluctuated between positive and negative net growth rates (-0.20–0.50 yr^{-1}). The power of such large-scale observations is the ability to identify areas of management concern and to frame questions that address the controlling mechanisms that influence these regions of fluctuating population growth.

There is a general agreement that anthropogenic alteration of the environment has influenced most areas on earth. Shallow marine ecosystems, including seagrass beds, have been no exception. Despite the recognition of seagrass beds as some of the world's most productive and valuable ecosystems, anthropogenic losses of seagrass beds continue at an alarming rate (Short and Wyllie-Echeverria 1996). Although anthropogenic seagrass losses have been attributed to many causes (e.g., dredging, filling, oil spills, and water diversion), most such losses result from human inputs of nutrients and sediment into the coastal zone (Short and Wyllie-Echeverria 1996). The mechanism of this eutrophication-associated seagrass loss is clear: nutrients cause a shift in plant species dominance from slow-growing seagrasses to faster-growing competitors and, in turn, to epiphytes, macroalgae and phytoplankton (Duarte 1995). The extensive losses of seagrass beds in the past few decades have focused attention on the need for fast, reliable methods and tools to evaluate the expansion or decline of seagrass populations.

Traditionally, seagrass distribution and health have been assessed by long-term mapping surveys with concurrent estimates of biomass and density (e.g., Orth and Moore 1983;

Quammen and Onuf 1993). The time course of changes in seagrass communities caused by eutrophication can be decadal (Fourqurean et al. 1995), resulting in slight year-to-year changes in the ecosystem. Unfortunately, mapping methods generally suffer from lack of precision because of spatial and seasonal heterogeneity and sampling error; for this reason, mapping techniques generally require long intervals to detect changes and necessitate repeated assessments of areas to ascertain trends. Recently, Duarte et al. (1994) have advocated the use of reconstructive population demographic methods to detect population growth trends. These methods rely on the ability to age individual short shoots (SS) of seagrasses by counting leaf scars and applying a plastochron interval (PI, Erickson and Michelini 1957). The age-frequency distribution of SS is a reflection of recruitment and mortality of individual SS to the seagrass population. A potential advantage of this approach is that estimates of recruitment and mortality can be obtained from a single sampling event. Previous examinations of seagrass population growth dynamics that used the PI and reconstruction method have consisted primarily of censuses on small spatial scales (0.1–1 km; e.g., Gallegos et al. 1993; Duarte et al. 1994; Durako 1994; Jensen et al. 1996). It is possible, however, that the reduced sampling effort of the reconstructive techniques compared with repeated mapping may permit regional-scale (hundreds of km), multiyear observations on seagrass population growth dynamics (e.g., Marbà et al. 1996).

The application of these techniques to populations of seagrass SS has not been generally accepted (*see* Durako and Duarte 1997; Jensen et al. 1997). Jensen et al. (1996) argue that the required assumptions of constant age-specific mortality and recruitment rates are untenable. They also express concern that durations of PIs can exhibit considerable spatial and temporal variation resulting from environmental influences. Recently, Kaldy et al. (1999) reiterated this concern and discouraged the use of the plastochron method for con-
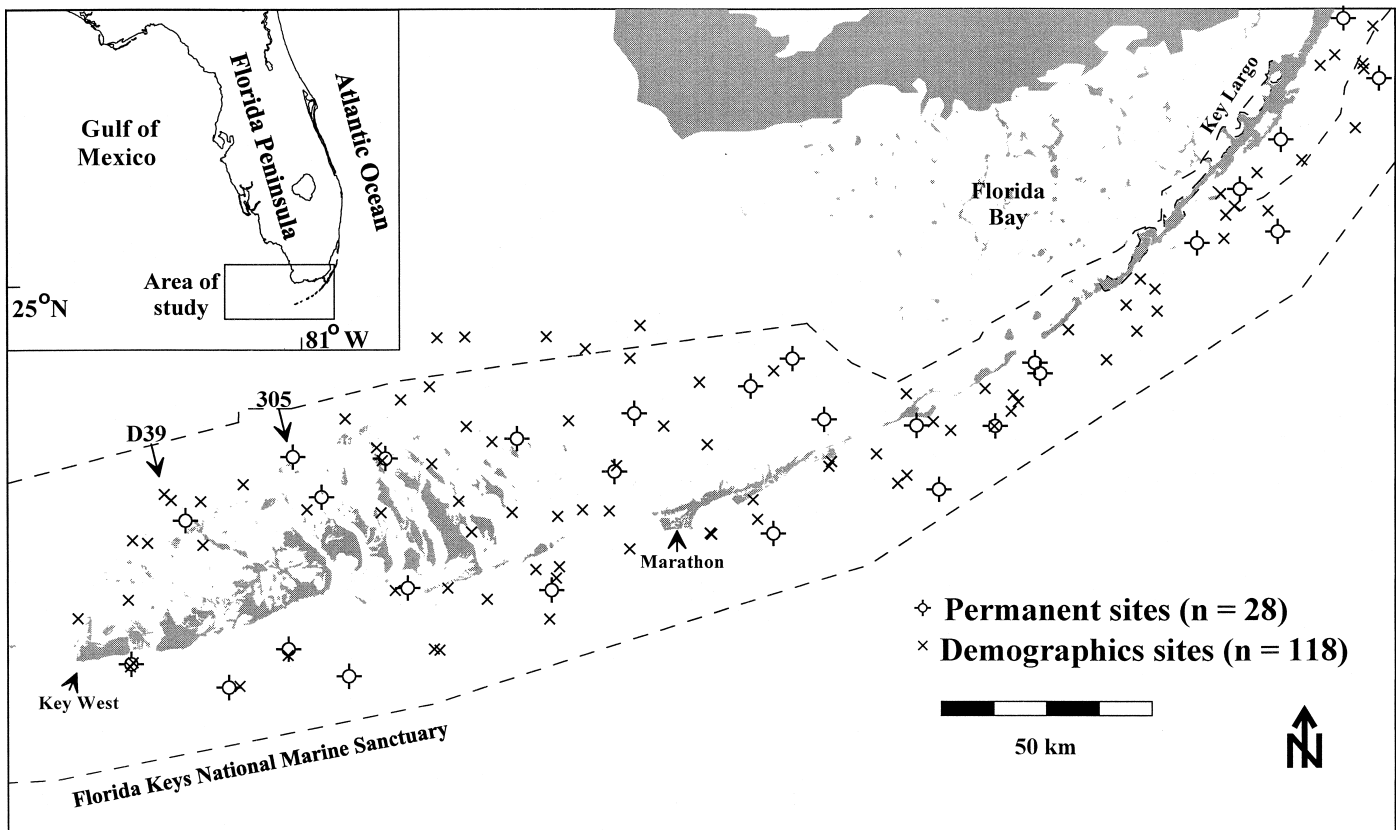
Fig. 1.   Site locations of *T. testudinum* SS demographic samples for 1996 and 1997.

struction of age-frequency distributions of *Thalassia testudinum*, because this species violated the assumption of equal elapsed time between successive leaf formation. Kaldy et al. (1999) further proposed that this bias in leaf formation measurements leads to the commonly reported seagrass age-frequency distributions with too few young shoots to account for the older shoots in the populations.

In this study, the potential of the PI–reconstructive demographic techniques to regional assessments of the state of seagrass populations was explored. In addition, we attempted to address the concerns raised by critics of the approach and reassessed the mathematical models used to derive recruitment and mortality from the age-frequency data. Data from a regional, multiyear, quarterly sampling program was used to assess spatial and seasonal variability in PIs. Then the temporally and spatially variable estimates were applied to collections of SS of *T. testudinum* from throughout the region, to estimate population growth parameters for the subpopulations. Although questions remain about the applicability of the reconstruction method as a tool for predicting change in seagrass populations, we believe that this technique can be used with caution to examine regional differences in population dynamics of seagrass beds.

Methods

The Florida Keys National Marine Sanctuary (FKNMS) consists of ~9,500 km² of coastal and oceanic waters that

extend from the southern tip of Key Biscayne to include the Dry Tortugas. For the most part, these 9,500 km² support seagrass communities; Fourqurean et al. (in press) document that there are >15,000 km² of seagrass beds in the south Florida region.

Leaf emergence rates—The rate at which new leaves were produced by SS was determined by leaf punching all SS within six 0.04 m² quadrants quarterly at 28 permanent sites within FKNMS in 1996 and 1997 (Fig. 1). These 28 sites correspond to a concurrent program of water quality monitoring and were chosen by use of a stratified-random approach, where distance offshore and broad geographic locations were the strata. After periods of 9–15 d, all SS within the quadrants were harvested. The leaf emergence rate (LER, in new leaves SS^{-1} d^{-1}) was calculated by dividing the number of new leaves produced in the incubation period by the total number of leaf-punched SS, then dividing by the time interval between marking and harvest. Note that LER is the reciprocal of PI, or the number of days between formation of successive leaves on a SS (Patriquin 1973; Brouns 1985). To evaluate the effects of seasonal variation on the estimates of LER, a sine-wave function (Eq. 1) was fitted to the data on leaf emergence rates acquired from the permanent quarterly sites by use of nonlinear least-squares regression:

$$LER = \overline{LER} + Amp[\sin(DOY + \phi)], \qquad (1)$$

where $\overline{LER}$ is the mean annual PI, *Amp* is the amplitude of

the sine wave, *DOY* is the day of year in radians, and ϕ is the phase angle. This equation was fitted to LER rather than to PI because LER approaches 0 in the winter months; hence PI approached ∞, which caused instability in the nonlinear regression.

Population demographics: determining age structure—During the summers of 1996 and 1997, samples of *T. testudinum* to be used in demographic analyses were obtained from 118 randomly selected sites within the FKNMS (Fig. 1). Samples from both years were quasi evenly distributed throughout our study area. Populations of SS were collected from each site by excavation of a sod, $\sim$1 m², that contained >100 SS. Care was taken to excavate the entire root-rhizome complex within a sod, but SS sometimes broke from the rhizomes. There is some possibility that inclusion of these broken SS in our analyses would lead to the underestimation of the age of those SS. Most of the time, however, this break occurred at or very near the rhizome, and we rarely observed broken SS still attached to the rhizome, so we felt that SS not attached to the rhizome could be included in our age-frequency estimations. Not including broken SS in the sample could also lead to a bias, because we noted that older, longer SS were more likely to break off their rhizomes than younger, shorter SS. The sods were placed in mesh bags, where the sediment was gently washed from the root-rhizome complex. Samples were returned to the laboratory for processing. The number of leaves produced over the lifespan of each SS in a sample was determined by counting leaf scars and extant green leaves. SS age was estimated by the number of leaves produced by a SS, scaled by the site-specific annual leaf production rates (Patriquin 1973; Duarte et al. 1994). This site-specific leaf production rate was calculated by interpolating the site-specific *LER* from the 28 permanent stations by use of a kriging algorithm.

Population demographics: reproductive effort—During 1997, the number of flowers, fruits, and rhizome apical meristems in each demographic sample was recorded. No attempt was made to determine sex ratio. The percentage of SS carrying flowers or fruits was determined, to examine the sexual reproductive effort. With this method, there is an inherent underestimation of sexual reproduction, because it only records the fruit and flowers present at the time of sampling; however, this was an attempt to discover any patterns of sexual reproductive effort in space. Because sampling occurred over a short time interval during the summer of 1997, we believe that the bias was uniformly applied across all sites. In addition, the number of horizontal rhizome apicals as a percentage of the total number of SS were determined to examine the asexual reproductive effort at each site.

Population growth rates: per capita mortality—Age-frequency distributions of SS were constructed for each demographic site. Instantaneous mortality rate, derived from the number of SS in each age class, was estimated by fitting the equation

$$N_t = N_o e^{-Mt} \qquad (2)$$

to the age-frequency distributions at each site, where N_o is

the estimated number of SS in the youngest age class, N_t is the number of SS in the tth age class, and M is the per capita mortality rate. Every age class contributed to the estimate of M. This calculation assumes (1) age-independent mortality, (2) constant annual SS mortality, and (3) constant annual recruitment rates. All of the SS age classes were used to estimate M instead of the numbers in cohort peaks, as has been used elsewhere (Durako 1994). We feel that this avoids biasing the estimate of M by only sampling individuals recruited to the population during cohort peaks; our method also allows for an analysis of the residuals to determine cohorts, although this was not applied in the present study.

Population growth rates: per capita recruitment—Gross recruitment was estimated from the age-frequency distributions by first estimating the number of new SS produced in the population within the last year and dividing by the total number of SS. For this to properly estimate gross recruitment, mortality of SS aged <1 yr must be accounted for; hence, we calculated gross recruitment (R_{gross}) as

$$R_{\text{gross}} = \frac{\sum_{j=1}^{k} e^{(\ln n_j + M t_j)}}{N}, \qquad (3)$$

where n is the number of SS in the jth age class, t is the age of the jth age class, k is the oldest age class <1 yr old, M is the per capita mortality rate, and N is the total number of SS in all age classes. Previous estimates of gross recruitment from seagrass age-frequency distributions (e.g., Duarte et al. 1994; Durako 1994) have not taken mortality of the aged SS <1 yr into account. Note that this calculation of gross recruitment is also dependent on the assumptions of age-independent mortality and constant interannual mortality.

Gross SS recruitment and mortality rates were used to calculate population growth as net annual new SS production,

$$P_{\text{net}} = R_{\text{gross}} - M, \qquad (4)$$

which predicts whether the population is expanding ($R_{\text{gross}} > M$), declining ($R_{\text{gross}} < M$), or in steady state ($R_{\text{gross}} = M$). In assessing spatial pattern in R_{gross}, M, and P_{net}, we treated samples collected in both sampling years as part of the same statistical population; in effect, this is explicitly recognizing the assumptions of the demographic models that R_{gross} and M are constant through time. Interannual variation in R_{gross}, M, and P_{net} will be explored in a future article.

Results

Leaf emergence rates—LER was measured in 210 out of a possible 224 times (28 sites $\times$ 8 sampling intervals); the differential was due to storm damage, lost data, and minor delays in establishing some sites. Measured LER ranged from a minimum of 0.0016 to a maximum of 0.0650 leaves SS⁻¹ d⁻¹, which translates into PI estimates of between 15.4 and 611 d leaf⁻¹. The mean LER was 0.0295 ± 0.0128 leaves SS⁻¹ d⁻¹ ($\pm$1 SD). The frequency distribution of PI estimates was skewed and failed tests of normality; the median PI was 34.7 d leaf⁻¹.
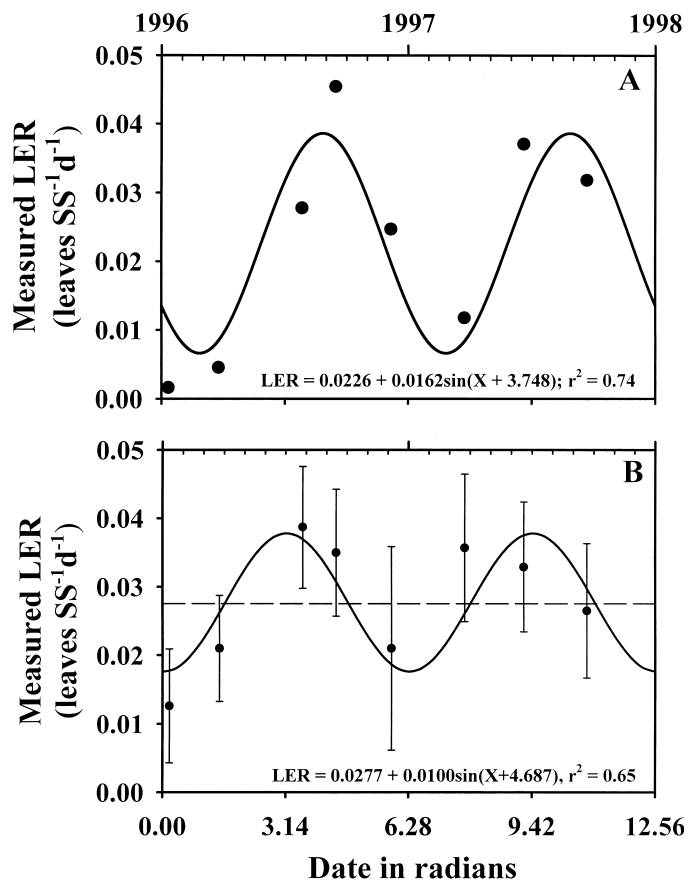
Fig. 2.   LER for *T. testudinum.* (A) Example data from one of the permanent stations (Sta. 314, see Fig. 1 for location). (B) The mean LER from all permanent stations (nominally *N* = 28). Error bars are 1 SD. Solid line represents a nonlinear least-squares fit of the sine model (Eq. 1) to the data. The bottom X axis is time of year in radians; the top X axis converts radians to months. The dashed horizontal line is $\overline{LER}$ from the model fit.

The sine model (Eq. 1) described the site-specific temporal pattern of LER quite well (*see* example data set, Fig. 2A). An average of 38% of the variance in LER at a site was described by the model, and in all 28 instances the parameter estimates for $\overline{LER}$ and *Amp* were significantly different from 0 at $P \leq 0.10$. The mean of the estimated $\overline{LER}$ from the 28 sites was 0.0296 $\pm$ 0.0046 leaves SS^{-1} d^{-1}, with a range of 0.0221–0.0406 leaves SS^{-1} d^{-1}. Mean annual leaf emergence rates were normally distributed about the mean (inset, Fig. 3). The mean estimated *Amp* was 0.0098 $\pm$ 0.0050 leaves SS^{-1} d^{-1}, with a range of 0.0018–0.0183 leaves SS^{-1} d^{-1}. There was a bimodal distribution of *Amp* estimates (inset, Fig. 3). There was spatial heterogeneity in the estimates of both model parameters (Fig. 3), with no clear relationship between $\overline{LER}$ and *Amp* or between these parameters and obvious physical factors, such as light availability and depth (nonsignificant linear regressions; data not shown).

As an alternative method of describing the general pattern in LER, the sine model (Eq. 1) was also fitted to the mean LER at all sites for each sample time (Fig. 2B). When the model was applied to these means, asymptotic 95% confi-

dence intervals (CI) for the parameters were 0.0218–0.0335 leaves SS^{-1} d^{-1} for $\overline{LER},$ 0.0013–0.0187 leaves SS^{-1} d^{-1} for *Amp,* and 3.873–5.500 for ϕ. The phase angle indicates the timing in the annual peak and nadir in LER; adding $3\pi/2$ to the value in radians and converting from radians to calendar dates yields an estimate of the timing of the peak production of new leaves between 14 May and 17 August and the timing of the minimum production between 13 November and 15 February.

Population demographics: determining age structure—In general, the 118 sites sampled for the age structure of *T. testudinum* SS were found to have populations that were skewed toward young individuals, with apparent cohort peaks approximately every 10 leaf scars (Fig. 4A,B). There were large ranges, however, in the predominance of young SS among the sites. The median number of leaf scars on SS from a sample ranged from 20 to 284 scars SS^{-1}, with a mean for all 118 sites of 53.5 $\pm$ 26.3 scars SS^{-1} (Fig. 5A). There was similar variability in the maximum number of leaf scars found on an individual SS at a site, with a range of 39–566 scars SS^{-1} and a mean of 103.6 $\pm$ 52.5 scars SS^{-1} (Fig. 5B).

The interpolated fields of $\overline{LER}$ calculated from the measured LER from the 28 permanent sites (Fig. 3) were used to estimate $\overline{LER}$ at all of the 118 demographics sites. These average annual rates of leaf emergence were used to convert the leaf scar count data from each demographic site into SS ages (Fig. 4C,D). The average median and maximum age of SS at a site were 5.0 $\pm$ 2.6 and 9.7 $\pm$ 5.1 yr, respectively (Fig. 5C,D). Spatial plots of median SS age revealed that the oldest subpopulations of *T. testudinum* occurred on the Atlantic Ocean side of the Florida Keys throughout the extent of FKNMS, whereas subpopulations on the Gulf of Mexico side of the Florida Keys had younger mean SS age (data not shown). Thus, the oldest populations existed offshore, and SS age decreased along a gradient from offshore to Florida Bay.

Population demographics: reproductive effort—An examination of the horizontal rhizome apical meristems per SS revealed a maximum level of asexual reproductive effort at 25%, with a mean of 8.3% $\pm$ 5.5 (1 SD) over the extent of the FKNMS (insert, Fig. 6A). In contrast, the greatest level of sexual reproductive effort was 25%, with a mean of 2.3% $\pm$ 5.0% (1 SD). The frequency histogram for SS that bore fruits or flowers was highly skewed, revealing that low levels of sexual reproduction occur throughout the extent of FKNMS. Thus, the average level of asexual reproductive effort in the FKNMS is four times greater than that of sexual reproductive effort (insert, Fig. 6B). Spatially, the populations with the greatest asexual reproductive effort occurred predominately on the Gulf of Mexico side of the Florida Keys and adjacent to the northeastern Florida Keys oceanside (Fig. 6A), whereas the populations with the highest sexual reproductive effort occurred on the ocean side of the Florida Keys, with four spatially coherent regions having levels >10%, located offshore of Key Largo, Lower Matecumbe, Summerland, and west of Key West (Fig. 6B). The highest levels of asexual reproductive effort and sexual re-
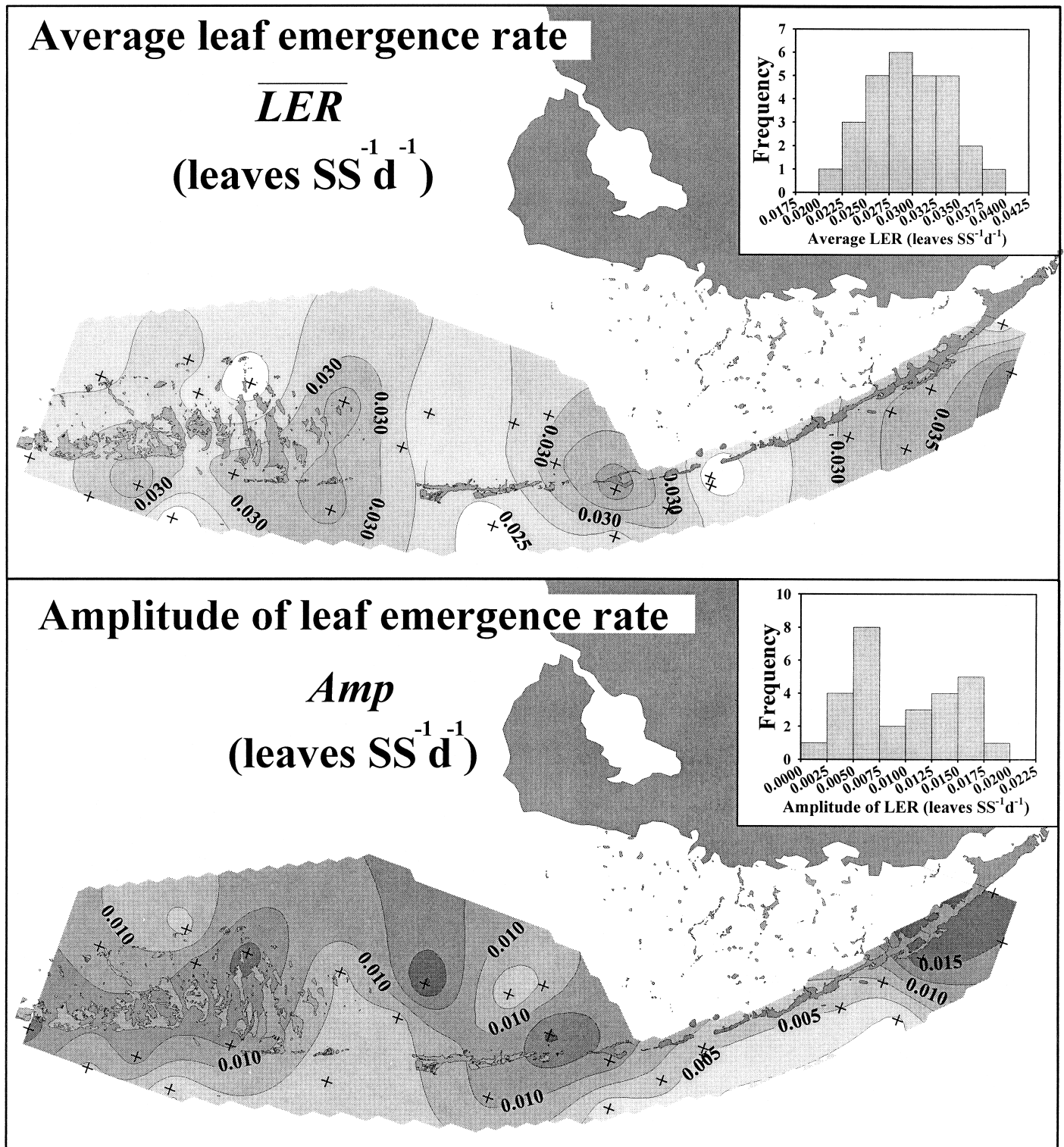
Fig. 3. Spatial pattern in $\overline{LER}$ (top) and *Amp* (bottom) for *T. testudinum*. Frequency distributions for each parameter are in the insets, $N = 28$. Station locations are indicated by small crosses. Note that the contour maps indicate the spatial extent of the study, not the limits of *T. testudinum* distribution in south Florida.
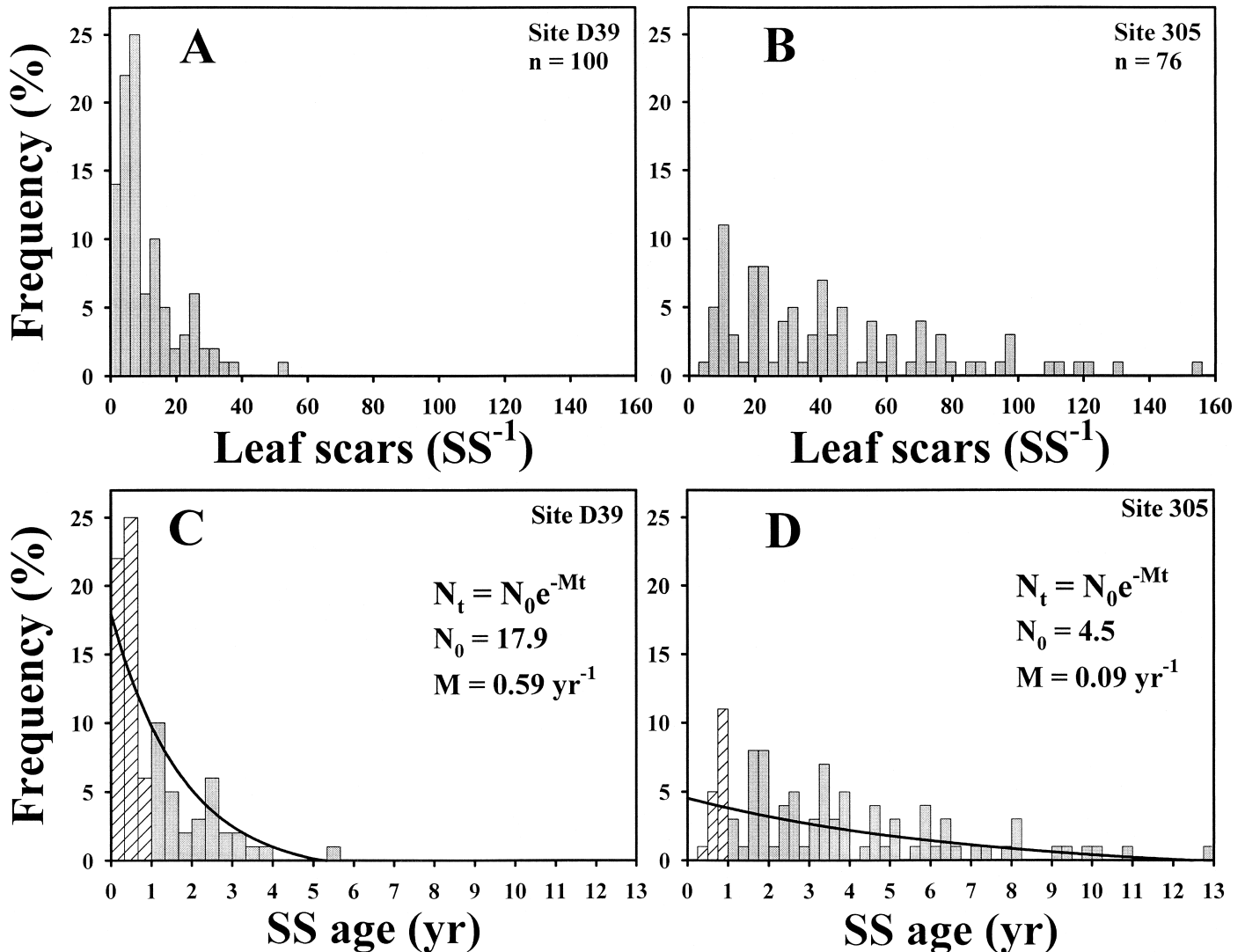
Fig. 4. Leaf scar and SS age frequency histograms from a high and low mortality site in FKNMS. (A) Leaf scar frequency histogram for site D39. (B) Leaf scar frequency histogram for site 305. (C) Frequency histogram of SS age for site D30. (D) Frequency histogram of SS age for site 305.

productive effort occurred in different spatial regions of FKNMS.

Population growth rates: per capita recruitment and mortality—Comparisons of the population growth parameters indicate significant demographic differences across the span of FKNMS. Estimates of R_{gross} for the 118 subpopulations of *T. testudinum* sampled ranged from 0.01 to 1.30 yr^{-1} (insert, Fig. 7A), with a mean of 0.17 ± 0.12 yr^{-1}. Spatially, the highest R_{gross} was found within Florida Bay north of Marathon (Fig. 7A). In general, annual recruitment increased from offshore to nearshore oceanside of FKNMS. Gross recruitment and asexual reproductive effort were significantly positively correlated (Fig. 8), but R_{gross} and sexual reproductive effort were not correlated.

As with R_{gross}, mortality of SS also ranged from 0.01 to 1.30 yr^{-1}, with a mean of 0.18 ± 0.09 yr^{-1}. In a pattern similar to that of R_{gross}, mortality rates increased from off-

shore to Florida Bay, with a peak in mortality north of Marathon (Fig. 7B). Thus, the greatest levels of R_{gross} occurred in areas of FKNMS that experience the greatest levels of mortality (Fig. 9).

Regional pattern in predicted net population growth— Predicted net population growth (P_{net} in Eq. 4) for the 118 subpopulations of *T. testudinum* from the FKNMS varied from −0.20 to 0.50 yr^{-1}, with a mean (−0.006 ± 0.089 yr^{-1}) that was not significantly different from 0 (inset, Fig. 10). This indicates that, on the whole, the *T. testudinum* population in the region is in steady state, but individual subpopulations are dynamic. Two distinct regions of net population growth and decline were evident (Fig. 10). Our analyses predicted expanding subpopulations of *T. testudinum* offshore between Marathon and Bahia Honda and in the far western extent of Florida Bay. Furthermore, we predicted that *T. testudinum* subpopulations were declining offshore of Planta-
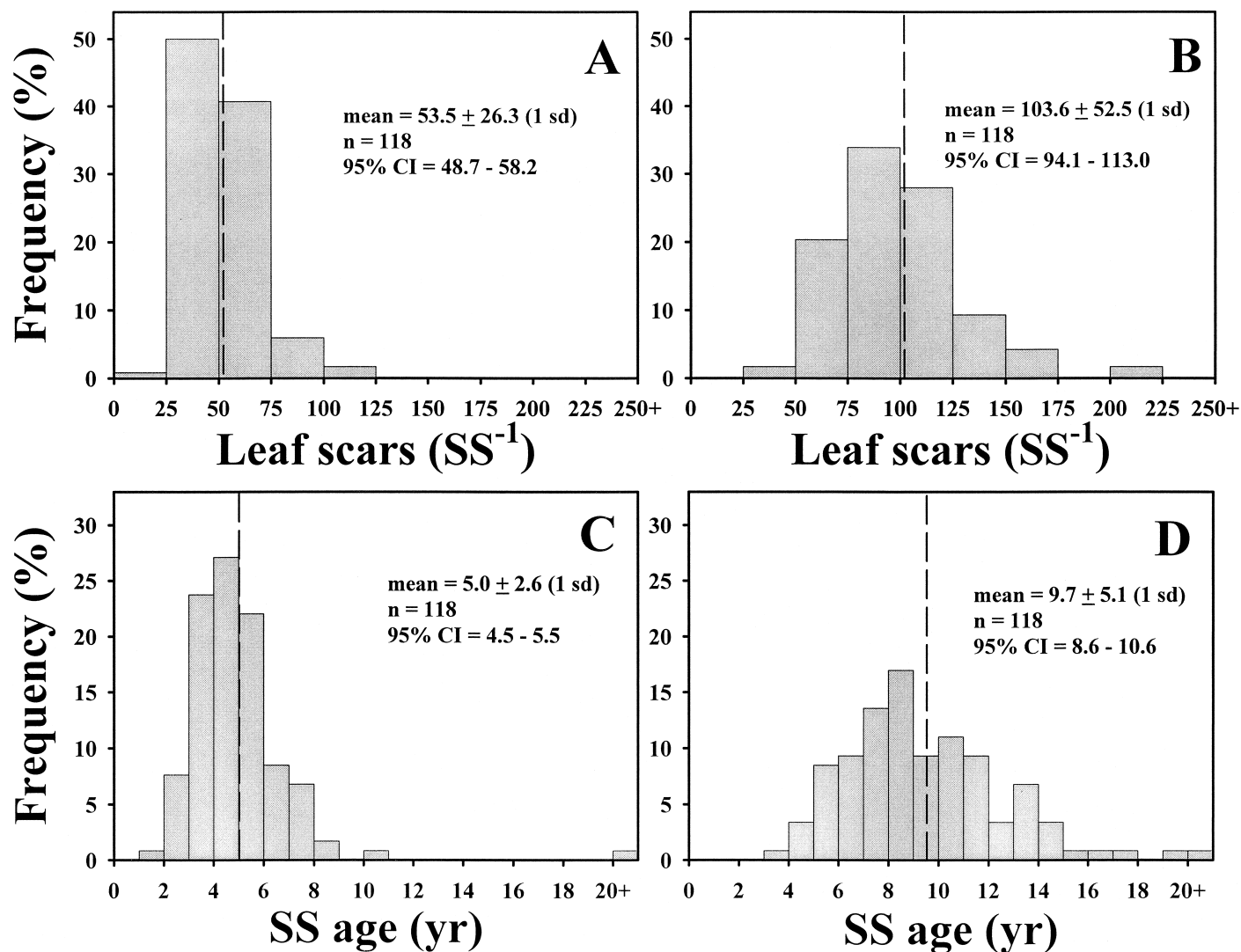
Fig. 5. Median and maximum leaf scar and SS age frequency histograms. (A) Median leaf scar frequency histogram. (B) Maximum leaf scar frequency histogram. (C) Median SS age frequency histogram. (D) Maximum SS age frequency histogram.

tion and Upper Matecumbe Keys and within Florida Bay north of Marathon and Bahia Honda. However, these predictions of net population change generated from our analysis of the age-frequency distributions of SS within subpopulations remain to be tested.

Correlation of environmental parameters with demographics data—At 22 of the permanent sites, several environmental parameters measured for another study (Fourqurean et al. 2001) could be correlated with the demographics data presented here. These parameters included depth, light reaching the bottom, seasonality of *T. testudinum* areal productivity, seasonality of *T. testudinum* standing crop, mean *Syringodium filiforme* standing crop, and seasonality of *S. filiforme* standing crop. There was no correlation between depth and mortality, recruitment, or net population growth ($P = 0.08$, 0.48, and 0.74, respectively). Nor was there a correlation between light reaching the bottom and mortality, recruitment, or net population growth ($P = 0.15$, 0.28, and

0.91, respectively). There was a positive correlation between depth and the sexual reproductive effort ($P = 0.03$), which indicates that those *T. testudinum* meadows at deeper sites had greater numbers of flowers or fruits. In addition, there was a positive correlation between maximum leaf scars and mean *S. filiforme* standing crop, as well as between median leaf scars and mean *S. filiforme* standing crop. This indicates that the oldest populations of *T. testudinum* in these permanent sites occur in areas where *S. filiforme* standing crops are greatest.

Discussion

The ability to determine the age of an organism has proved useful in elucidating its ecology and population dynamics. A population age structure is simultaneously the outcome of past demographic events and an indication of its demographic future. The current population age structure reflects previous temporal variation in recruitment and mor-
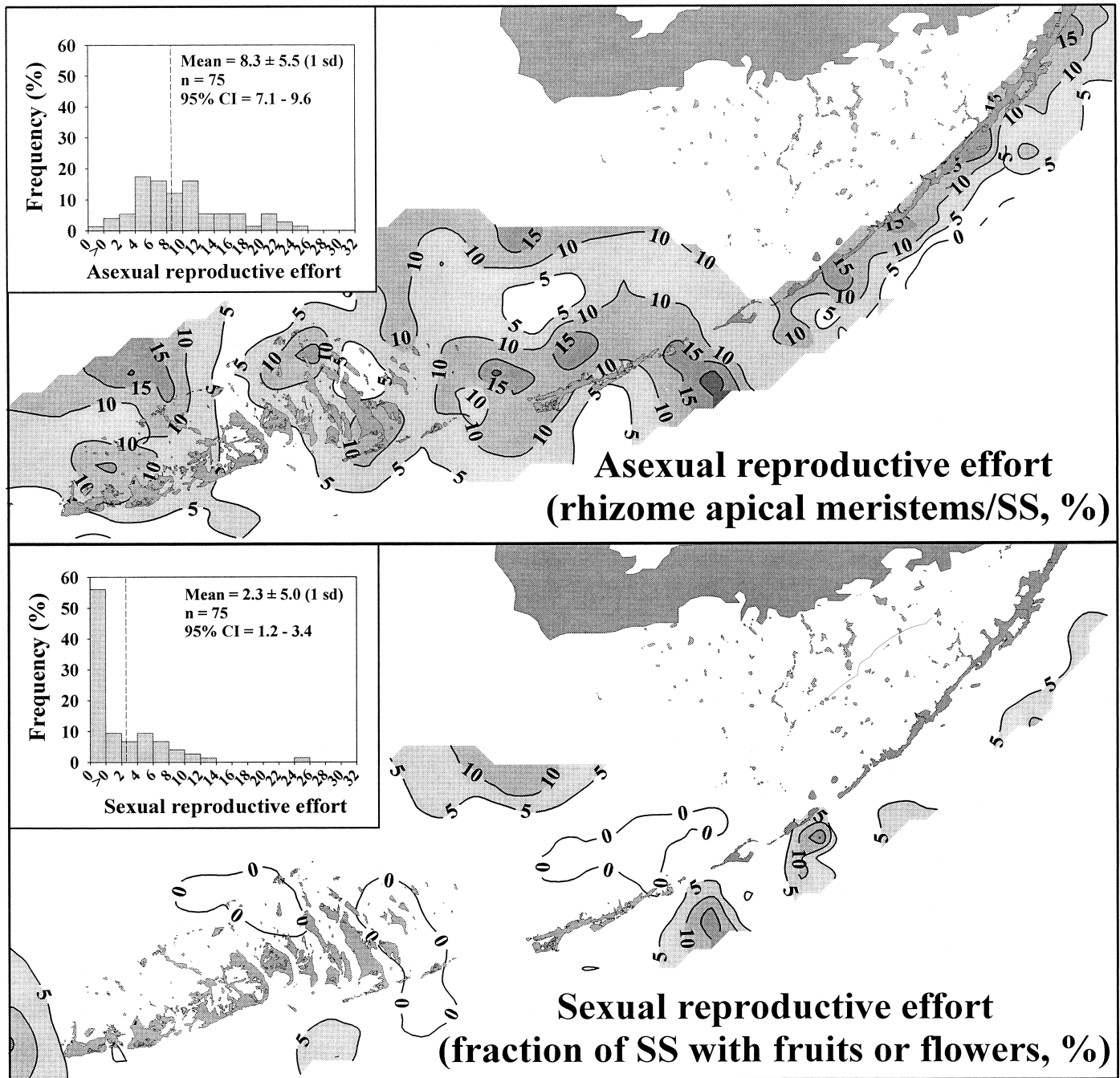
Fig. 6. Spatial pattern in asexual reproductive output (top) and sexually active SS (bottom) throughout the extent of FKNMS. Frequency histograms for asexual reproductive output (insert, top) and sexually active SS (insert, bottom) are shown.

tality and can predict future population growth (Caswell 1989; Bullock et al. 1996). Hence, the ability to determine the age of shoots of *T. testudinum* provides a powerful tool for clarifying population dynamics of this species (Gallegos et al. 1993; Duarte et al. 1994; Durako 1994). Although techniques for determining the age of seagrass shoots have been available for the past three decades (Patriquin 1973), they have only recently been used extensively. As these tools are exercised more frequently, the techniques continue to improve. In the present study, we have accounted for sea-

sonality in leaf emergence rates and applied refinements in the extraction of demographic parameters from age-frequency distributions. We have also used these techniques for the analysis of the demographics of *T. testudinum* over an unprecedented spatial scale and have documented large-scale patterns in shoot demographics.

As noted by critics of reconstructive aging techniques (Jensen et al. 1996; Kaldy et al. 1999), LERs, critical to the conversion of leaf-scar information into age, are not constant in either space or time. We documented considerable varia-
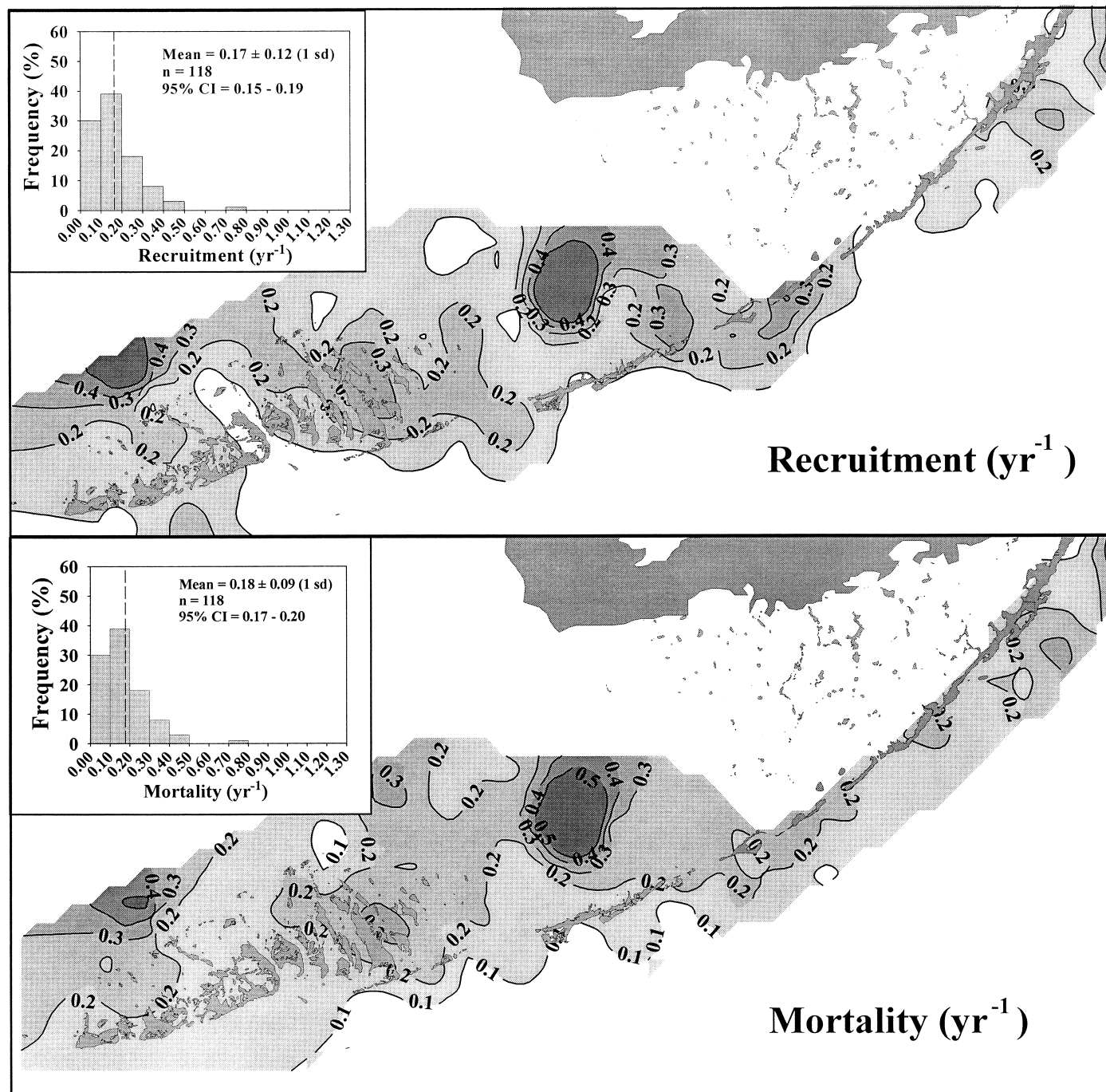
Fig. 7. Spatial pattern in annual recruitment (top) and mortality (bottom) over the extent of the FKNMS. Frequency histograms of recruitment estimates (insert, top) and mortality estimates (insert, bottom) at the 118 sites with the mean and 95% CI are shown.

tion in LERs across our study area (Fig. 3): it is imperative that site-specific measures of LER rate be used when calculating the ages of SS. We also applied a novel approach for incorporation of seasonal variation in LERs into an estimate of yearly average LER ($\overline{LER}$). We fitted a sine model to time series of measured LERs; this allowed for calculation of both a yearly mean ($\overline{LER}$) and a measure of seasonal variation (*Amp*). The amplitude of the yearly signal in the LER of *T. testudinum* was ~33% of the mean in south Flor-

ida (Fig. 2B). For comparison, we applied our sine model to the data on intra-annual variation in leaf emergence rates in Puerto Morelos, Mexico (Gallegos et al. 1993), and Laguna Madre, Texas (Kaldy et al. 1999). In Puerto Morelos, a more tropical location than south Florida, the sine model estimated $\overline{LER}$ for three sites to be between 0.035 and 0.041 leaves SS^{-1} d^{-1}, with *Amp* varying from 0.004 to 0.017 leaves SS^{-1} d^{-1}; the amplitude of seasonal variation was 24% of the mean. In Laguna Madre, a less tropical location than south
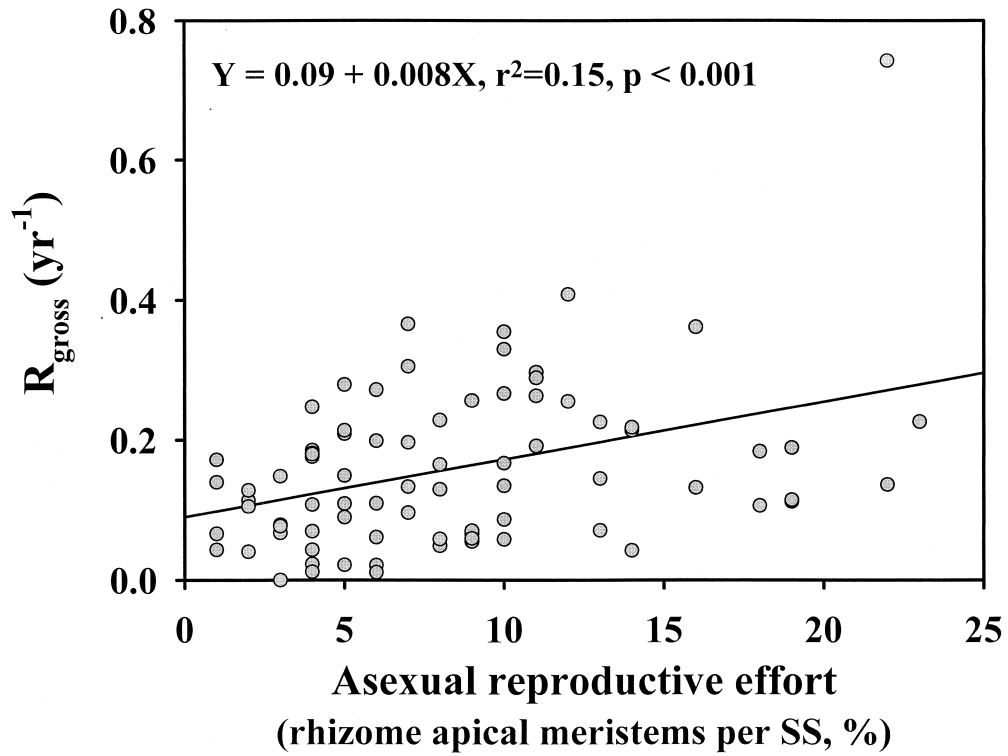
Fig. 8.   Relationship between *T. testudinum* gross recruitment (yr^{-1}) and asexual reproductive effort (%) at 118 sites in south Florida.
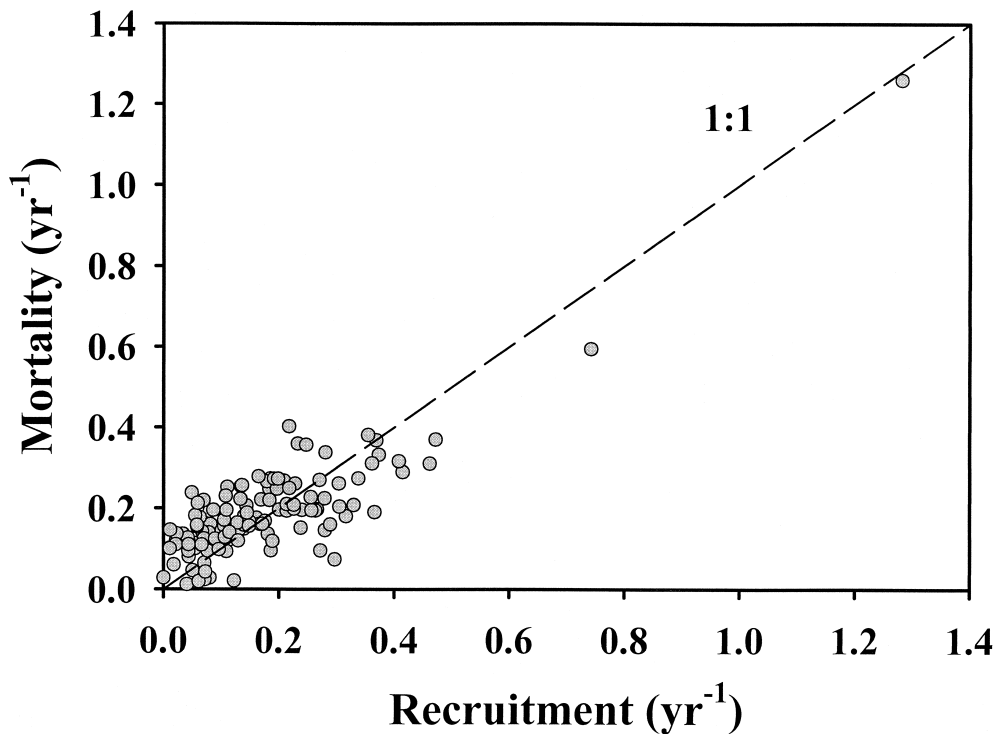

Fig. 9.   Scatter plot of estimated mortality and gross recruitment for *T. testudinum* subpopulations from 118 sites in south Florida.
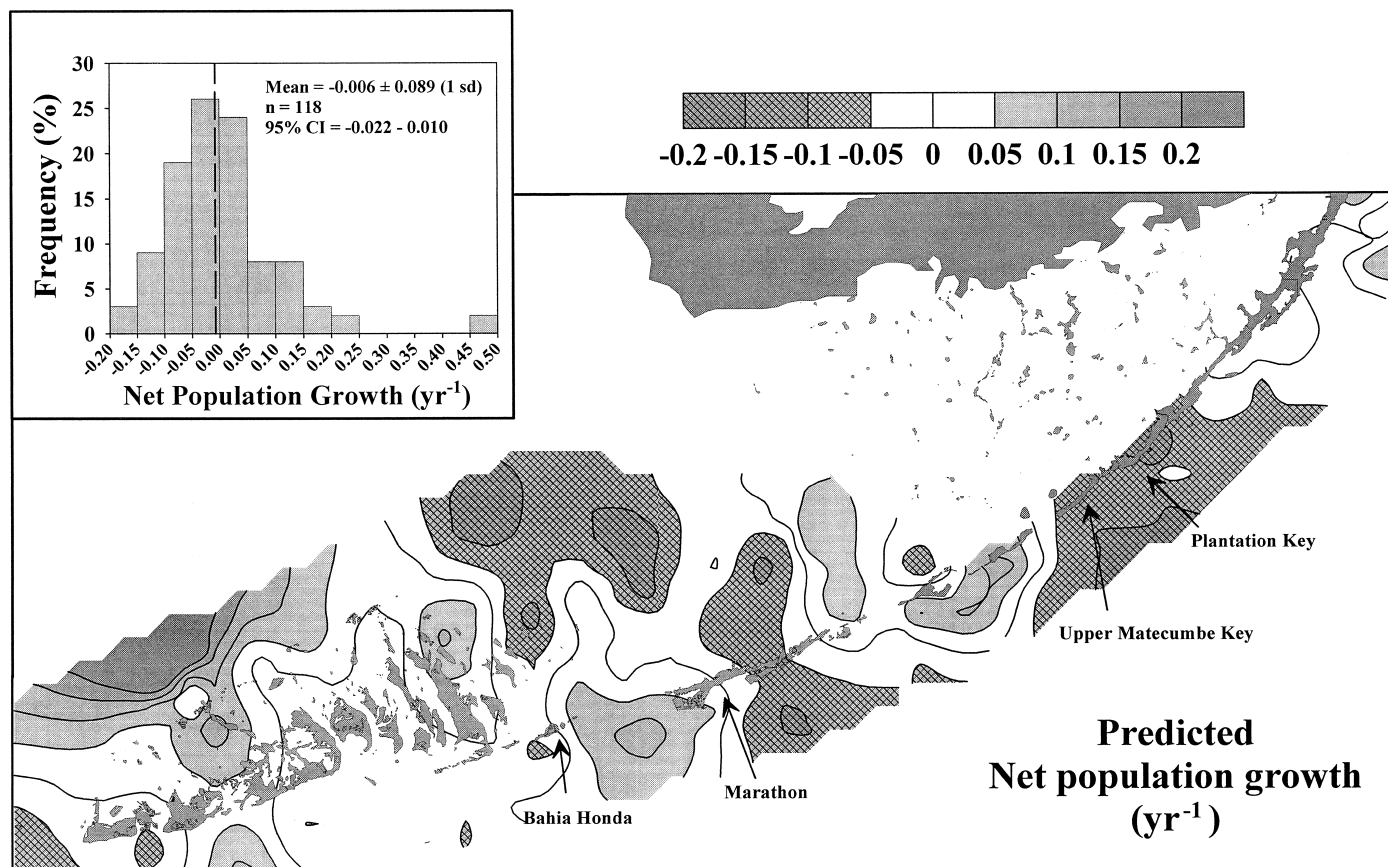
Fig. 10. Spatial plot of the predicted net population growth of *T. testudinum* within the boundaries of the FKNMS. Frequency histogram of the estimated net population growth for the 118 samples with mean and 95% CI is shown as the insert.

Florida, the amplitude of seasonal variation was 43% of the $\overline{LER}$.

We propose that the use of an annual $\overline{LER}$ is an improvement of the seagrass demographic and reconstruction technique over other estimates of LER. In the work presented here, there were no significant differences in the average LER measured across time at a site and the estimate of $\overline{LER}$, because our sampling events were evenly distributed in time. However, the estimates of $\overline{LER}$ from the sine model may be much different than the simple average if the sampling events are not evenly spaced in time. The calculation of an annual estimate of $\overline{LER}$ incorporates the potentially considerable temporal variation in productivity resulting from fluctuating environmental influences, which has been expressed previously by some investigators as an obstacle to applying reconstructive techniques (Jensen et al. 1996; Kaldy et al. 1999).

The average yearly mean $\overline{LER}$ found in this study predicts a PI of 34 d for *T. testudinum* in south Florida. This value is high in comparison with the 13–18 d found by Durako (1994) in an examination of *T. testudinum* SS age structure in Florida Bay; it is also higher than the average of 15.6 d reported in a review of the literature on this species (Duarte 1991). This discrepancy is most likely a result of earlier estimates of PI that were based on few measurements concentrated during late spring and early summer, the period of

peak leaf emergence (Fig. 2). Summer estimates of PI for *T. testudinum* from the literature are all quite short, with PI generally <20 d (Table 1). In contrast, studies that have assessed PI on an annual basis produce longer estimates of PI, from 21 d in the Yucatan to 187 d in the northern Gulf of Mexico (Table 1); our estimates are within this range. On the other hand, there may be real biological reasons that Durako (1994) could have found a shorter PI than our estimates. Durako was studying the effects of the poorly understood seagrass die-off in Florida Bay, and he noted that there was a pattern of decreasing PI concurrent with increasing magnitude of disturbance. In effect, PI decreased in his study as the seagrass canopy was thinned, which possibly indicates a growth response to the thinning canopy. Indeed, sparse SS that survived drastic canopy thinning had PI values as short as 4 d (Durako 1994). It is also possible that our sampling regime missed peak times of leaf emergence because of lowered leaf emergence as a consequence of summer sexual reproduction (as documented by Kaldy et al. 1999). However, the low rate of sexual reproduction measured in this study (Fig. 6B) argues against this contention.

In addition to the use of an annual estimate of $\overline{LER}$, we modified the gross recruitment equation to incorporate mortality of shoots aged <1 yr. Previously (Duarte et al. 1994), gross recruitment was calculated by the equation

Table 1. Comparison of plastochron interval (PI) estimates for *Thalassia testudinum* from a variety of locations derived from leaf marking. Some measurements were made only once, during late spring to early summer, whereas others represent yearly means.

PI (d leaf^{-1} ss^{-1})	Location	Latitude (N)	Reference
Measurements made during summer			
12	Bermuda	32°17′	Patriquin (1973)
13–18	South Florida	25°	Durako (1994)
14–16	South Florida	25°	Zieman (1975)
20–47	South Florida	24°30′	Tomasko and Lapointe (1991)
20–27	Belize	18°	Tomasko and Lapointe (1991)
11–20	Barbados	13°10′	Patriquin (1973)
Annual estimates			
187	Northern Gulf of Mexico	30°	Eleuterius (1987)
29–38	Texas	26°10′	Kaldy et al. (1999)
25–50	South Florida	24°30′	Present study
21–26	Yucatan, Mexico	21°	Gallegos et al. (1993)
27–29	Yucatan, Mexico	20°30′	van Tussenbroek (1995)

$$R_{\text{gross}} = \ln \sum S_{\text{total}} - \ln \sum S_{t+1}, \qquad (5)$$

where S_{total} is the total number of SS in a sample and S_{t+1} is the number of SS aged >1 yr. Equation 5 does not account for the loss of new recruits during the year into an estimate of gross recruitment. Obviously, mortality occurs within shoots <1 yr old. We propose that our modified gross recruitment equation (Eq. 3) more accurately reflects what occurs within natural seagrass populations. Comparison of estimates of gross recruitment generated by Eq. 3 with those calculated by Eq. 5 revealed that Eq. 3 leads to a significant increase in the estimation of gross recruitment. On the basis of the 118 subpopulations of *T. testudinum* in this study, Eq. 3 resulted in an increase in estimated gross recruitment that ranged from 1% to 56%, with a mean increase of 13%. Of particular interest is that the difference between the two methods increases as R_{gross} increases. Therefore, use of Eq. 5 results in greater underestimations of gross recruitment in subpopulations that experience higher levels of recruitment and mortality. Although questions remain about the validity of the assumptions required by the reconstructive technique, our modifications will improve the estimates of shoot age, annual mortality, annual recruitment, and, consequently, net population growth.

Analysis of the population age structure of 118 subpopulations of *T. testudinum* throughout the extent of FKNMS over a 2-yr period revealed significant spatial variation in SS demographic characteristics and in the predicted population dynamics. There was a spatial overlap of the populations with the highest asexual reproductive effort (Fig. 6A) and high R_{gross} (Fig. 7A) in Florida Bay and the Upper Keys but not throughout the rest of FKNMS. Similarly, a less dramatic overlap of populations with high sexual reproductive effort with high mortality existed in the Upper Keys and one region of the Florida Bay. A significant correlation between populations with high asexual reproductive effort and R_{gross} (Fig. 8) and between populations with R_{gross} and high mortality (Fig. 9) existed over the study area. Throughout the extent of FKNMS, sexual reproductive effort did not correlate to R_{gross} ($r^2 = -0.012$, $P = 0.908$) or to asexual reproductive effort ($r^2 = 0.021$, $P = 0.102$). Thus, we conclude that asexual vegetative growth drives recruitment

dynamics in south Florida within the boundaries of the FKNMS.

An attempt to correlate the estimated *T. testudinuim* population demographic parameters to environmental data revealed that there were no statistically significant relationships with depth or light reaching the bottom. This lack of correlation suggests that the amount of light reaching the bottom is not a primary controller of recruitment and mortality of *T. testudinum* in south Florida. It is possible some as-yet-unexamined physical parameter may correlate with SS mortality and recruitment. For example, seasonality in the productivity of *T. testudinum* appears to be related to seasonality in water temperature in south Florida (Fourqurean et al. 2001). Furthermore, small-scale physical disturbances (e.g., ''blowouts,'' Patriquin 1975) can create variability in the species composition and possibly demographics of seagrass beds; this could obscure relationships between demographics and other environmental driving variables. In addition, biotic interactions may attribute to the spatial variability of *T. testudinum* population growth in south Florida. Several recent studies have demonstrated that herbivory of seagrass can increase shoot density and seagrass productivity in the northern Gulf of Mexico and south Florida (Valentine et al. 1997, 2000), or herbivory can totally disrupt the previous age structure of the population (Rose et al. 1999). All of these possible factors have yet to be tested. Currently, we are examining whether the estimates of recruitment and mortality calculated in the present study accurately reflect the population growth dynamics of *T. testudinum* in subsequent years.

Discrete areas of high and low mortality and high and low recruitment were observed in FKNMS. The spatial patterns of high gross recruitment and high mortality were nearly congruent. Thus, the greatest risk of mortality occurred in areas where gross recruitment was highest. This pattern has been shown elsewhere for perennial and annual terrestrial plants (Bullock et al. 1996; Noble and Dirzo 1997) and is likely a result of intraspecific competition. It is possible that the increased density due to new recruits increases the mortality rate as a result of reduced light levels caused by shading or reduced per capita nutrient availability. Alternatively,

the reduced density caused by mortality may enhance recruitment. However, regardless of the mechanism, it is noteworthy that estimating gross recruitment with Eq. 5 increasingly underestimates recruitment as recruitment increases and that, in FKNMS, the gross recruitment was positively correlated with mortality. Thus, the use of Eq. 5 would substantially underestimate P_{net} in these areas and predict negative net population growth in very dynamic seagrass subpopulations.

The unprecedented scale of examination undertaken in the present study allowed regional observations of *T. testudinum* population dynamics. Our demographic analyses indicated that the net population density of *T. testudinum* over the breadth of FKNMS was stable, because the mean estimated P_{net} was not statistically different from 0. However, age structures of populations suggests that areas within FKNMS fluctuate between positive and negative net growth rates. Smaller observations in isolated areas might lead to opposite conclusions about the overall state of *T. testudinum* populations in FKNMS.

We believe that the changes proposed in this study for estimating an annual PI and calculating gross recruitment are improvements to the reconstruction technique and should be considered in future studies. In addition, we suggest that the assumptions of this technique be tested experimentally. Although the validity of the assumptions used in the reconstructive technique for seagrass is still debatable and use of the calculated population parameters to predict future trends in populations is still largely untested, the power of such large-scale observations is in their ability to identify areas of management concern and to shape questions about the controlling mechanisms that influence these regions of fluctuating population growth.

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