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Estimation of primary production using five different methods in a *Spartina alterniflora* salt marsh

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Abstract

The aboveground production of *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana, USA was estimated using five different harvest methods: peak standing crop (PSC), Milner-Hughes, Smalley, Wiegert-Evans, and Lomnicki *et al.*, and a non-destructive method based on measurement of stem density and longevity. Annual production estimates were 831 ± 41, 831 ± 62, 1231 ± 252, 1873 ± 147 and 1437 ± 96 g dry wt m^{-2} for each method, respectively. The average longevity of individually tagged young shoots was 5.2 ± 0.2 months, equivalent to an annual turnover rate of 2.3 crops per year. Among the five methods, Wiegert-Evans and Lomnicki *et al.* were considered more accurate than the other three because they corrected for mortality losses between sampling times. The Lomnicki *et al.* method was preferred over the Wiegert-Evans method because of its greater simplicity.

Introduction

As the base of a complex food web, the production of *Spartina alterniflora* salt marshes has been of increasing interest. This has led ecologists to estimate the production of these systems using methods which vary from simple to complex. Reviews of primary production in *S. alterniflora* dominated salt marshes by Keefe (1972), Turner (1976), Kirby and Gosselink (1976), Hopkinson *et al.* (1978), and Linthurst and Reimold (1978) show a wide range of production, the estimates depending partially on the choice of method. All but one field comparison of methods used to estimate production are from marshes along the Atlantic coast. Shew *et al.* (1981), the most complete study to date, compared five methods of estimating production from a single data set in a *S. alterniflora* salt marsh in southeastern North Carolina. Their results may not be directly applicable to the Gulf marshes because of the different seasonality, temperature, tidal regime, geology, and plant turnover rate.

In this Gulf of Mexico marsh study, we used the same five harvest methods as Shew *et al.* (1981) to compare production estimates: (1) peak standing crop (PSC); (2) Milner-Hughes (1968); (3) Smalley (1958); (4) Wiegert-Evans (1964); and (5) Lomnicki *et al.* (1968). A non-destructive estimate was also made from culm longevity and mean live culm biomass. Kirby and Gosselink (1976) conducted a similar study at Barataria Bay, Louisiana using all the methods except the Lomnicki *et al.* Hopkinson *et al.* (1978) studied a nearby area using only the PSC and Wiegert-Evans methods.

The objectives of this study were to compare the five methods of production estimation and to estimate annual plant turnover rate at the study area. We hypothesized (1) that techniques correcting for

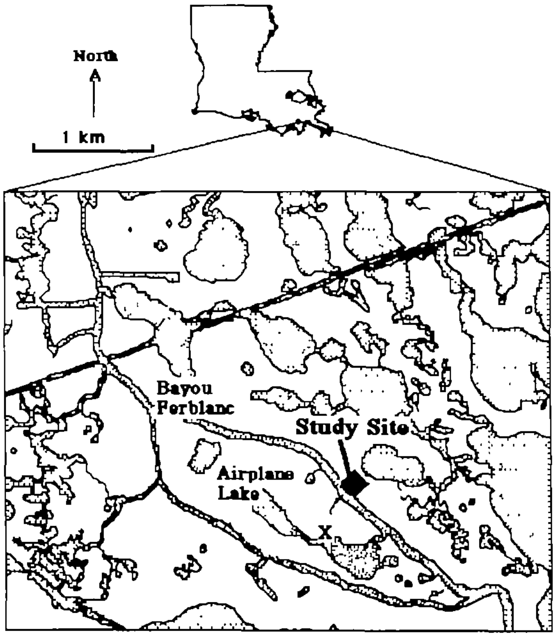

Fig. 1. Location of Airplane Lake, showing the sampling sites for this study (black square) and Hopkinson *et al.* (X).

mortality losses between harvests would give higher estimates of production than techniques that do not correct for these losses; and (2) that the differences among techniques would be larger in Gulf of Mexico than east coast sites because of the longer season, warmer winter, and hence larger turnover rate.

Materials and methods

We studied a *Spartina alterniflora*-dominated area located along Bayou Ferblanc, within 0.5 km of Airplane Lake in Barataria Bay, Louisiana (Fig. 1). About 95 to 99% of vegetation was *S. alterniflora* and the remainder was *S. patens*.

We sampled the aboveground *S. alterniflora* biomass every month from May 1980 to June 1981. On each sampling date, ten replicates were cut about 20 m apart, on a transect perpendicular to the bayou (Fig. 2). Although we recognized the possibility of a productivity gradient along the bayou, we chose this design in preference to a more random design because the latter would have required frequent access to the whole sampling site. In earlier studies (Kirby and Gosselink 1976; Hopkinson *et al.* 1978) we found severe disturbance, including death of vegetation, along paths between plots. The sampling site was visually homogeneous along the bayou. Each replicate was divided into four 0.25 m^2 quadrat-plots (A, B, C, and D) with a space of 0.5–1.0 m between plots. Plots A, B, C, and D were determined randomly, and sampled as described by Shew *et al.* (1981). On each sampling trip we removed from plot A all standing live and dead culms and litter, from plot B the live culms without disturbing the dead material, and from plot C dead culms and litter without disturbing the live material. Nothing was removed from plot D until harvest, one month later. Plot C and D were enclosed with 3 mm mesh hardware cloth screen wire cages (0.5 × 0.5 m^2 by 90 cm high) to reduce the lateral exchange of detritus that might increase the variability of dead biomass in the plots. On the next sampling trip, the dead culms and litter in plot B, and the live and dead culms and litter in plots C and D were harvested. Then a new set of A, B, C, and D plots was set up about 5 m downstream from the old ones.

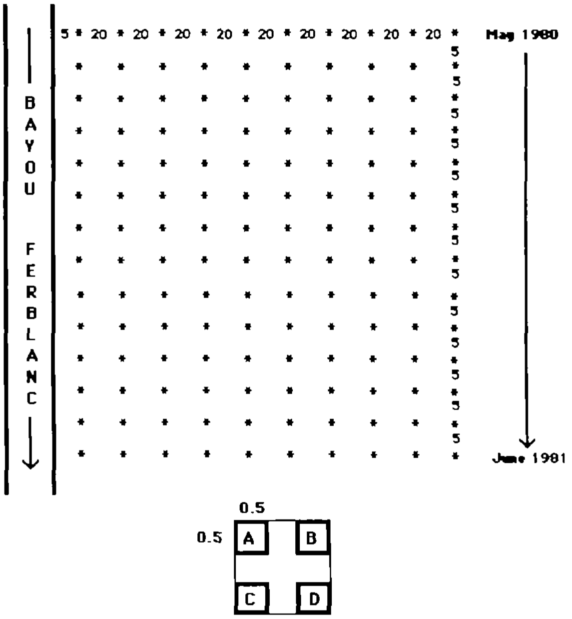

Fig. 2. Monthly sampling transects along Bayou Ferblanc. The asterisk (*) is the sampling site location. The distance between locations was 20 m along the transect and 5 m south (down) the next month. The square at the bottom is the sampling design for each location. A, B, C, and D were randomly determined; dimensions are in meters.

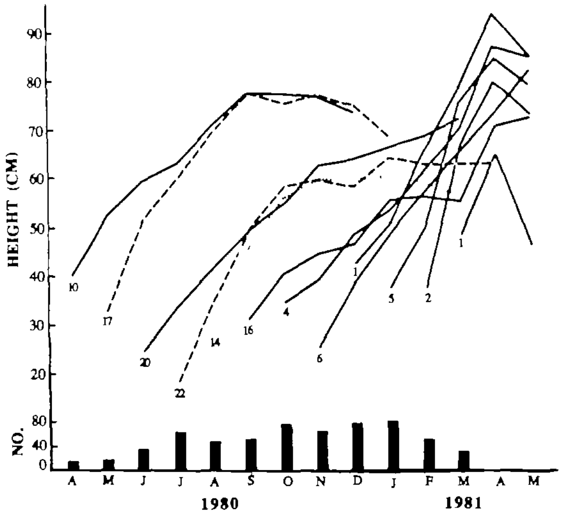

Fig. 3. Average height of culms tagged each month; curves end when the last culm is dead; number of culms initially tagged is beneath each line; solid, dashed, and dotted lines are used to distinguish different cohorts. Bar graphs are the numbers of culms < 25 cm tall per m².

We placed the plant material removed from each plot in plastic bags and, in the laboratory, separated material into live culms, dead culms plus litter, and dead parts that were removed from the live culms. Plant material was dried at 60°C to constant weight to the nearest 0.1 g.

We also tagged small live culms to determine their longevity and turnover rate. Twenty-five new culms of *S. alterniflora* were marked each month, and each was measured monthly to the tip of the tallest leaf until it was found dead. The culm turnover rate was calculated using the following equations:

$$\text{Turnover rate} = \frac{\text{Length of growing season (days)}}{\text{Average longevity (days)}}$$

$$\text{Average longevity} = \frac{\sum_{c=1}^{n} (\text{longevity (days)} \times \text{density of stems } (\#\text{m}^{-2}))}{\sum_{c=1}^{n} (\text{density of stems } (\#\ \text{m}^{-2}))}$$

where the growing season for *S. alterniflora* at the study area was 365 days, c = cohort, and n = months.

Table 1. Average density and longevity of *S. alterniflora* culms, and number of culms used to determine average longevity each month (1980–1981); 25 culms were tagged each month.

Month of tagging	Average density of culms less than 25 cm (# per m²)	Average longevity (days)	No. culms to determine avg. longevity
4	14.8	169	10
5	16.6	130	17
6	34.8	190	20
7	64.8	133	22
8	46.8	186	14
9	54.4	163	16
10	76.0	171	4
11	64.0	143	6
12	77.6	102	1
1	79.6	117	5
2	52.4	97	2
3	31.0	63	1

Results

Culm longevity and seasonal standing crops

Culms tagged in winter (December through March) had higher growth rates than culms tagged in other months (Fig. 3). The winter-tagged culms also appeared to live a shorter period (Table 1), but this conclusion is somewhat in question since the sample number in winter months was small. Based on the life spans of 118 individual culms, the average longevity (mean ± 1 std. error) of *S. alterniflora* culms at the study area was 5.2 ± 0.2 months (160 days) or 2.3 crops per year. This life span is shorter than those obtained by Shew *et al.* (1981) for *S. alterniflora* in a southeastern North Carolina salt marsh, which were 8.0 ± 0.4, 7.6 ± 0.4, and 8.1 ± 0.6 months for short, medium, and tall *S. alterniflora*, respectively. The culm longevity in this study was also less than estimated by Hopkinson *et al.* (1980), which was 7.4 months (222 days).

Live standing crop averaged 415 g dry wt m^{-2} and ranged from 62 g m^{-2} in February–March, to 831 g m^{-2} in July–August (Fig. 4). The total amount of dead material, consisting of the dead standing culms, litter, and the dead parts that were attached to the live culms, averaged 885 g dry wt

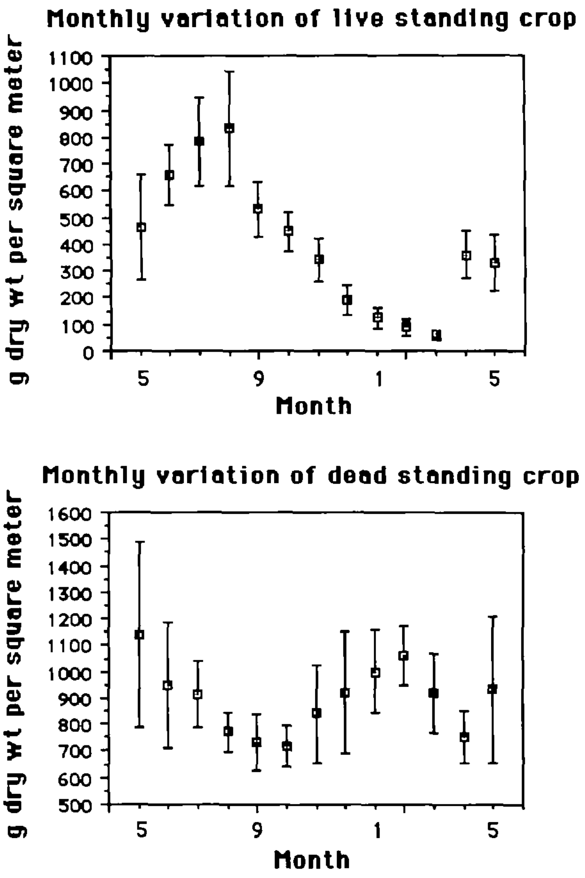

Fig. 4. Monthly variation of live and dead standing crop; the bars are standard deviations; the dead material includes litter and dead parts removed from live culms.

m^{-2} and ranged from 718 to 1138 g dry wt m^{-2} . The lowest value for dead material was recorded in September–October, and the highest value was, as expected, in January–February when live material was lowest.

There was no effect of screening on live or dead biomass. The removal of dead material from plot C at the beginning of each sampling seemed to reduce the standing stock of live material; after one month the live biomass in plot C was smaller than in plots A and D. Further, the removal of live material from plot B at the beginning of each sampling reduced the amount of dead material at the end of each sampling by about 18%.

When all samples were treated together, there was no detectable effect of distance along the transect from the Bayou Ferblanc on the amount of live and dead material. However, the highest dry weights were recorded at Replicate 1 next to the Bayou and Replicate 10, close to a relatively large body of water.

Production estimates

There was no difference in the amount of either live or dead material in plots A compared to D. Thus, we used the average values of A-dead and D-dead for Dead, and the average values of A-live and D-live for Live, in calculating production. When only A-live or D-live, and A-dead or D-dead was available, we used the mean of the available values. Otherwise, we used mean values of the ten replicates in the calculations (see Kaswadji 1982 or Shew *et al.* 1981 for a detailed description of each method).

We estimated the production of each of the 10 replicates and averaged them into mean production (mean ± 1 std. error). The estimates ranged from 831 ± 41 g dry wt $m^{-2}.yr^{-1}$ using PSC to 1873 ± 147 g dry wt $m^{-2}.yr^{-1}$ using the Wiegert-Evans method (Table 2). These estimates are higher than those Shew *et al.* (1981) obtained (241 to 1029 g dry wt $m^{-2}.yr^{-1}$) using the same method for a southeastern North Carolina *S. alterniflora* salt marsh. The difference agrees with the observations that salt marsh production is higher at lower latitudes (Turner 1976).

Monthly production estimates for the four methods indicate generally that production was relatively high in June, when the study started, then decreased to a minimum in September (Fig. 5). After that, the monthly estimates varied depending on method. The Milner-Hughes method simply measures the sum of all monthly positive live biomass increases. The results from this method indicate no production from September through March, a rapid increase the next month, and then a decrease in May. Months of no production are, of course, unrealistic because growth was observed in the tagging studies (Fig. 3).

The Smalley method corrects for mortality between samples by summing algebraically the change in live biomass and in dead biomass (negative totals are set to zero). Results using the Smalley method

Table 2. Summary of annual primary production and turnover rates for *Spartina alterniflora*; numbers in parentheses are the results if 'negative production' is counted as zero.

Methods	Primary production (g dry wt m^{-2}.yr^{-1})				Annual turnover rate (production to peak standing crop) for this study	Amount under (−) or over (+) estimate of turnover rate relative to calculated turnover rate (2.3) for this study
	This study[1]	Kirby and Gosselink (1976)[2]	Hopkinson *et al.* (1978)[3]	Shew *et al.* (1981)[4]		
Peak standing crop	831 ± 41	903	754	242	1.0	− 1.3
Milner-Hughes	831 ± 62	811	–	241	1.0	− 1.3
Smalley	1231 ± 252	1200	–	225	1.5	− 0.8
Wiegert-Evans	1873 ± 147 (2733 ± 235)	1988	2658	1029 (1038)	2.2 (3.3)	− 0.1 (+ 1.0)
Lomnicki *et al.*	1437 ± 96 (2046 ± 125)	–	–	1028	1.7 (2.5)	− 0.6 (+ 0.2)

[1] Transect across a mostly inland site.

[2] Average of streamside and inland sites.

[3] Intermediate streamside to inland marsh site.

[4] Short marsh.

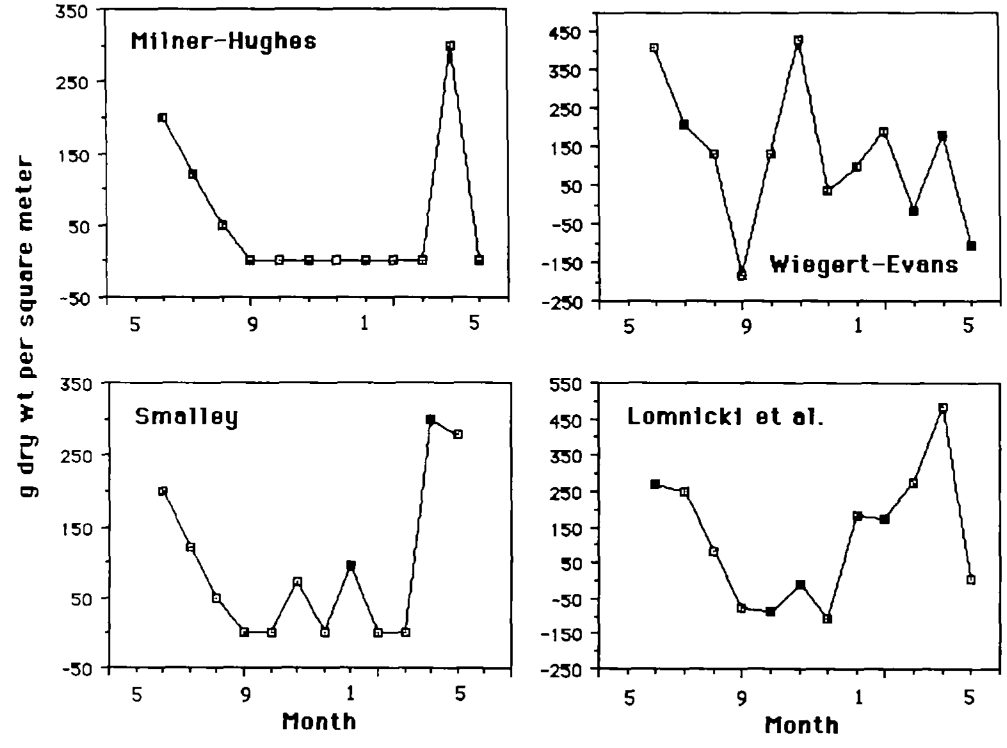

Fig. 5. Estimates of monthly production using the four different methods.

were similar to Milner-Hughes, with peak production in May, June, and July and low, variable production from September through March.

The Wiegert-Evans method calculates loss of dead material each month (from B plots), and adds that to the change in dead standing stock (A + D plots) to estimate mortality. Mortality, in turn is added to the change in live biomass (from A + D plots), to estimate production. Variability is generally high, and negative values can occur, presumably due to random variation. In order not to bias the results upward, these values were retained in the annual estimate. The Wiegert-Evans method estimated negative production in September, March, and May, with considerable month-to-month variation. The high production calculated in November contrasted with the other methods.

In the Lomnicki *et al.* method, mortality is estimated directly by the appearance of dead plant material one month after removal of all dead culms from C plots. As with the Wiegert-Evans method, monthly mortality is added to the change in live biomass to estimate production. The monthly production rates from the Lomnicki *et al.* method were negative from September through December. They were highest in April through July, with the exception of May. Negative net production does not occur, by definition. In this technique if no production occurs during a month, any mortality (loss of live biomass) should appear as dead biomass accumulation. Negative values represent both loss of dead biomass from C plots during the interval between samples and statistical variation among plots. Because setting negative values to zero may bias the production estimate upward, we retained those values.

Discussion

Production estimates

Peak standing crop method. The mean live standing crop for the month (August) when standing crop peaked in most plots, was 831 ± 41 g dry wt $m^{-2}.yr^{-1}$, which is comparable with results of both Hopkinson *et al.* (1978; 754 g $m^{-2}.yr^{-1}$), and Kirby and Gosselink (1976; 903 $gm^{-2}.yr^{-1}$). This method does not consider either production of live material after the seasonal peak, or the effects of mortality occurring between sampling events. Thus, this method usually underestimates true production, especially in low latitudes (Turner 1976).

Milner-Hughes method. Production estimated by this method was 831 ± 62 g dry wt $m^{-2}.yr^{-1}$, or about the same as the production estimated from PSC. Using the Milner-Hughes method, Kirby and Gosselink (1976) obtained 811 g dry wt $m^{-2}.yr^{-1}$ production for *S. alterniflora* in Airplane Lake, Louisiana. Since this method, like the previous one, does not account for mortality between sampling periods, it also underestimates production.

Smalley method. Production estimated using this method was 1231 ± 252 g dry wt $m^{-2}.yr^{-1}$. Kirby and Gosselink (1976), using the same method at Airplane Lake, recorded 1200 g dry wt $m^{-2}.yr^{-1}$ production for *S. alterniflora*. Turner (1976) noted that when live biomass is increasing between sampling periods, a possible underestimate of production one month may be corrected by an overestimate in the following months. But when live biomass is decreasing, the errors in the estimate of the actual production cannot be corrected. Smalley (1958) wrote that even if there were no statistical variations, the method would still underestimate production at times. Thus, although the calculation of production using this method is higher than the previous two methods, it also underestimates the actual production rate.

Wiegert-Evans method. This production estimate was 1873 ± 147 g dry wt $m^{-2}.yr^{-1}$. This method does not treat negative monthly values as zero as does the Smalley method, but treats them as 'negative production' in totaling annual production. 'Negative production' is assumed to be a statistical artifact resulting from the large error terms of the method of calculation. In the calculations, we included dead parts attached to the live culms as dead material. In one modification of the method that excluded the dead parts of live culms from the total dead material, Shew *et al.* (1981) found a 33.7% reduction of production. They concluded that if this dead material is excluded from the calculation, actual production is biased toward underestimation. Hopkinson *et al.* (1978) noted that in Louisiana, the production estimated using the Wiegert-Evans method is 2 to 4.4 times greater than peak standing biomass. The method is probably more accurate than the previous methods, because it corrects for mortality occurring between sampling periods, through consideration of the instantaneous rate of disappearance of dead material and changes in dead biomass between sampling times.

Lomnicki et al. method. Production estimated using this method was 1437 ± 96 g dry wt $m^{-2}.yr^{-1}$. This method used the dead material from plot C to estimate mortality between sampling times. There are no other studies of this method in Louisiana *S. alterniflora* stands for comparison. Compared to other harvest-based estimates, true net production should be represented best by the Lomnicki *et al.* method, because it is the most direct measurement of both biomass change and mortality. None of these methods correct for herbivory, which has been reported to be negligible in salt marshes (Smalley 1958).

Turnover rate

The culm turnover rate of *S. alterniflora* at the study area was 2.3 crops per year. Hopkinson *et al.* (1980) measured 2.9 crops per year in another Louisiana salt marsh. These two estimates were higher than the measured turnover rate of 1.5 for *S. alterniflora* in southeastern North Carolina (Shew *et al.* 1981).

We also calculated turnover rates using the ratio of annual primary production and standing crop (Table 2). Because the culms die after reaching their peak sizes, not their mean sizes, we used the peak live standing crop, not the mean live standing crop, in this calculation. Turnover rates based on the ratio of Lomnicki production to PSC and of Wiegert-Evans production to PSC were 1.7 and 2.2, slightly lower than the turnover rate calculated from stem tagging. Thus, based on the comparison of turnover rates, all estimates of primary production in this study were underestimates of actual production.

The tagging study shows that production was actually occurring during the winter (and that the negative values are therefore unrealistic). All stems tagged in late summer were growing during the fall-winter period; their growth rates were relatively high, and stem density in September through January was higher than the average monthly mean (Fig. 3). One possible source of error was the effect of clipping material from C and D plots, which may have influenced mortality and growth rates in undetermined ways.

Primary production rates in Louisiana marshes are up to two times higher than PSC, primarily because of the rapid turnover of plant biomass. The Wiegert-Evans and Lomnicki *et al.* methods provide the most accurate procedures for measuring plant production of the five methods examined, but data collection is labor intensive. Harvest measurement of PSC combined with non-destructive estimation of culm turnover rate is a less laborious method of estimating net primary production, that gives results comparable to Wiegert-Evans and Lomnicki *et al.* All three methods require repetitive sampling, on a maximum interval of four weeks, for reproducible results. Considerable savings in time and effort would result if turnover rates for a species could be reliably related to latitude.

The difference between the minimum and maximum estimates using the five methods was 787 g m^{-2} in North Carolina (Shew *et al.* 1981) and 1052 g m^{-2} in Louisiana (this study). The ratio of Wiegert-Evans production to PSC was 4.2 in North Carolina (Shew *et al.* 1981) but 2.2 in this study. A comparison of these turnover rates suggests that turnover rate increases with latitude, contrary to earlier views (Turner 1976). Since production estimates from PSC times turnover rate are sensitive to small changes in turnover rate, the wide range found in these studies argues against use of turnover rate for estimating production. We require more extensive data on turnover rates before they can be widely applied for estimating production.

Acknowledgments

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