

Production of Dominant Emergent Vegetation and of Pool Algae on a Northern Massachusetts Salt Marsh

Author(s): Ernest Ruber, Gregory Gillis and Paul A. Montagna

Source: *Bulletin of the Torrey Botanical Club*, Apr. - Jun., 1981, Vol. 108, No. 2 (Apr. - Jun., 1981), pp. 180-188

Published by: Torrey Botanical Society

Stable URL: <https://www.jstor.org/stable/2484897>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Torrey Botanical Society is collaborating with JSTOR to digitize, preserve and extend access to *Bulletin of the Torrey Botanical Club*

JSTOR

Production of dominant emergent vegetation and of pool algae on a northern Massachusetts salt marsh¹

Ernest Ruber, Gregory Gillis and Paul A. Montagna

Biology Department, Northeastern University, Boston, MA 02115

RUBER, E. (Northeastern Univ., Boston, Mass. 02115), GREGORY GILLIS (Bunker Hill Comm. Coll., Charleston, MA 02129) and PAUL A. MONTAGNA (Univ. South Carolina, Columbia, SC 29208). Production of dominant emergent vegetation and of pool algae on a northern Massachusetts salt marsh. *Bull. Torrey Bot. Club* 108: 180-188, 1981.—Cover frequency for the emergent vegetation of three representative sections of a salt marsh is presented. Annual production values are calculated using the ash-free dry weights of a series of harvests of standing live and dead crops, and estimating export or decomposition losses from the standing crops from data on litterbag-losses. Production values are provided for tall and dwarf *Spartina alterniflora*, *S. patens*, *Distichlis spicata*, *Juncus Gerardi*, *Salicornia europaea*, *Typha angustifolia* and *Scirpus olneyi*, the last two being based on end-of-season harvests only. These species account for from 88 to 96% of the emergent cover of these marsh sections. Salt marsh pool production and cover values are obtained and integrated for 8 months of the year. Such pools comprise from 0 to 26% of the sections studied. These data provide a baseline for studies of energy transfer in this marsh.

Key words: Salt marsh; Massachusetts; production; cover values; *Spartina*; *Distichlis*; *Juncus*; *Salicornia*.

Much early salt marsh ecology dealt with distributions of plant life types, species and societies and the determination of major environmental limiting factors (Chapman 1940; Miller and Egler 1950; Hinde 1954; Adams 1963). The description of successional patterns was also stressed and continues today largely in studies working out the mechanisms underlying such patterns (Blum 1968) or demonstrating new patterns (Ranwell 1974).

The work of Odum and de la Cruz (1967) culminated a series of ecosystem-oriented studies by Odum and co-workers (referenced in the above cited work). Odum and de la Cruz offered evidence for the export of particulate detritus from a Georgia salt marsh. The presumed importance of detrital material to the survival of coastal

fisheries resources led to a number of studies evaluating material and energy flow in these systems. Among these were plant production studies as reviewed by Keefe (1972), work on plant decomposition rates which have been extended and reviewed by Montagna and Ruber (1980) and continued attempts to measure materials flux (Murray 1978, and several papers in Wiley 1976).

Much of the previous work was done south of Cape Cod and tended to interpolate basic data from other areas. Approaching New England the most integrated work was that of Nixon and Oviatt (1973) in Rhode Island. Other work stressed special phenomena such as pollution effects on plant production (Valiella *et al.* 1975) on the south side of Cape Cod or thermal effects (Vadas *et al.* 1976) in Maine. To our north we are aware only of the work of Vadas and the studies of Hatcher and Mann (1975) in Nova Scotia on *Spartina alterniflora* production.

We decided that the Parker River National Wildlife Refuge and its adjacent marshes offered an opportunity to do an integrated study of a northern salt marsh ecosystem. Also, we chose to concentrate on a more elevated marsh than usual and to investigate more intensively the small

¹Work on the Parker River National Wildlife Refuge was conducted under permits 5-PRR-72-17, 74-14, and 78-2. We are grateful to George Gavutis and Al Zelley for cooperation. Work in private adjacent areas was conducted with kind permission of Mr. and Mrs. W. Hopkins. We are grateful for the occasional help of a number of others, particularly Alan Bronstein, supported by a Federal work-study grant and Elaine Tomlinson supported by the Northeastern University Cooperative Education Program. Dr. Harold Stubbs gave use valuable advice on the statistics.

Received for publication October 5, 1979.

pool communities of the marsh which had been hitherto largely ignored. In this paper we provide data on cover and production of surface and pool plants on this marsh.

Materials and methods. The marsh is in the township of Rowley, Massachusetts. Three sections, designated areas A, B and C (Fig. 1) were selected for this study because their drainage characteristics were definable for other portions of our study (Montagna and Ruber 1980; Murray 1978; and Bronstein and Ruber 1979, presentation before New England Estuarine Research Society).

Plant composition was censused by walking a series of transects and lowering a point-cover sampling frame (Greig-Smith 1964) at predetermined intervals of 5 or 15 m according to the size of the area censused. Area A was censused by 8 transects totaling 82 quadrats, each quadrat having 10 sample points. An aerial photograph was used to determine the total area, (16,150 m²) of which 26% is occupied by a pool. Area B (66,250 m²) was censused by 5 transects (65 quadrats). Area A and B transects ran on North South axes, from upland to upland

this being demarcated by the disappearance of *Spartina patens* and *Juncus Gerardi*. Area C (108,600 m²) was censused by transects from the upland to a series of channels, and along a border defining the limits of the drainage area of a major marsh channel. Seven transects totalling 270 quadrats were made.

Net production of marsh dominants was obtained from standing crop harvest and decomposition estimates. Standing crop was harvested on 5 dates. Eight replicate quadrats randomly placed in areas of almost pure stands were harvested. The quadrat sizes were for the tall *Spartina alterniflora* (TSA) ecophene, 0.25 m²; for dwarf *S. alterniflora* (DSA), *Spartina patens* (SP), *Distichlis spicata* (DS) and *Juncus Gerardi* (J) 0.1 m²; and for *Salicornia europaea* (S) 0.04 m² since available stands of the last were much smaller. Despite the smaller quadrat sizes, standard errors of the mean remained comparable with those obtained from the larger quadrat sizes (Table 2).

Typha angustifolia and *Scirpus olneyi* were sampled on only one date, 7 September 1978, for peak standing crop. Four quadrats of 1.0 m² each were clipped for both species. These are important species in fresher areas of the marsh, but not in areas A, B or C (Table 1). Their data are included here only for the record.

Plants were dried for 48 hours at 60°-80°C, weighed and then incinerated for 4 hrs at 550°C to determine organic content (ash-free dry weight). Estimates of losses to decomposition and export were obtained by placing numbers of 5 mm mesh plastic litterbags, with known amounts of *S. alterniflora*, at different marsh sites and collecting, drying and weighing the residuals after different intervals (details in Montagna and Ruber 1980).

Production and decomposition values were integrated using the rationale which was summarized and extended by Kirby and Gosselink (1974). In this scheme an attempt is made to assess changes in live, and dead standing crop, together with losses to decomposition, export and herbivory thus:

$$P = \Sigma[\Delta L + (\Delta D + E + De)] + H$$

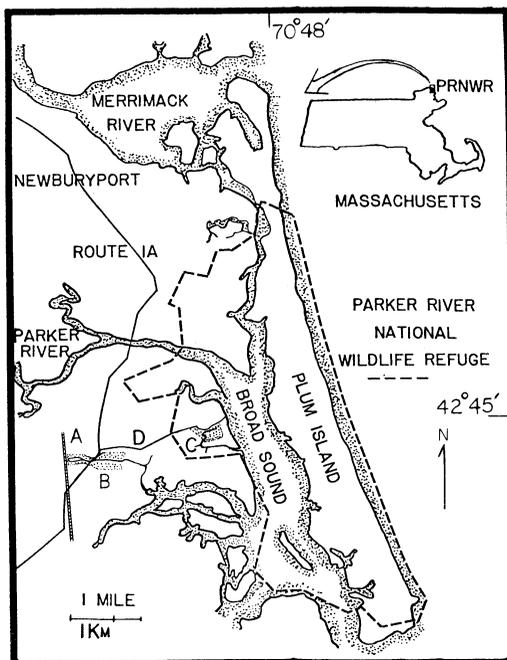


Fig. 1. The Parker River National Wildlife Refuge and adjacent study areas. Study areas A, B and C are lettered and stippled for location. D is Stackyard Road.

Table 1. Percent cover of three sections of salt marsh by emergent plants and topographic features.

Species or feature ^a		Area A	Area B	Area C
<i>Spartina alterniflora</i>				
Tall	X ^b	—	4.9	7.0
Intermediate		9.9	*	.6
Dwarf	X	6.4	16.0	24.9
<i>Spartina patens</i>	X	25.5	19.9	45.6
<i>Distichlis spicata</i>	X	17.2	29.4	8.8
<i>Juncus Gerardi</i>	X	3.3	12.1	.4
<i>Salicornia europaea</i>	X	1.2	2.8	.5
Pools	X	26.0	—	7.9
<i>Atriplex patula</i>		.1	1.4	.3
<i>Iva frutescens</i>		1.7	1.4	.3
<i>Limonium Nashii</i>		.3	*	.1
<i>Solidago sempervirens</i>		.7	3.5	*
<i>Spergularia marina</i>		* ^c	*	*
<i>Suaeda maritima</i>		*	.3	*
<i>Triglochin maritimum</i>		.1	*	.3
<i>Elymus virginicus</i>		—	.6	—
<i>Festuca rubra</i>		—	.3	.1
<i>Juncus effusus</i>		*	1.2	—
<i>Panicum virgatum</i>		1.8	*	—
<i>Polygonum</i> sp.		—	.3	—
<i>Spartina pectinata</i>		—	.5	—
<i>Teucrium canadense</i>		—	1.4	—
<i>Typha angustifolia</i>	X	.8	—	*
Bare ground		3.2	.9	.5
Channels		1.8	3.1	2.7

^a The first 8 categories comprise 88–96% of the cover, the next 7 are common but sparse; and the following 8 are mainly brackish-water or upland edge forms.

^b X = we have production data for the category.

^c * = present but not in sample quadrats.

where P is net primary production in gms. ash-free dry-weight $m^{-2} yr^{-1}$, L and D are the changes in live and dead standing crops, E and De are export and decomposition, respectively, all measured at chosen intervals during the growing season and summed. The term in parenthesis ($\Delta D + E + De$) is ignored if it is negative under the assumption that the predicted export and decomposition loss is already incorporated in the larger loss of dead standing crop. There are generally no salt marsh data for herbivory (H) except those of Smalley (1959) from Georgia. We use his data which place herbivory at about 7% of primary production.

Salt marsh pool production was measured by use of light and dark bell-jars (Pomeroy 1959) with changes in dissolved oxygen measured by the azide modification of the Winkler technique (Anon. 1965). One pool was studied intensively with measurements made from April through November. Replicate jars were set up contain-

ing a section of floating algal mat (fm) of the same area as the jar ($641 cm^2$); the bottom was covered by a polyethylene sheet to exclude contributions from benthic species. It was assumed that plankton productivity is negligible beneath the floating mat since these mats range from 5–25 cm in thickness. Plankton productivity was obtained from jars (pl) with both the floating mat and the benthic contributions excluded (pl). Benthic contributions were obtained from jars overlying the benthic algal mats, excluding floating mats, but including plankton (bm). Thus, the monthly production rates (P) for the separate producer compartments are:

$$P_{fm} = (P_{fm} \cdot C) - (NR_{fm} \cdot C)$$

$$P_{pl} = P_{pl} (1 - C) - NR_{pl}$$

$$P_{bm} = (P_{bm} - P_{pl}) (1 - C) - (NR_{bm} - NR_{pl})$$

and p represents the mean net daily rates of production ($mg O_2 m^{-2} day^{-1}$) of each bell-jar type, multiplied by 30 or 31 to get monthly rates. C is the mean percentage of

Table 2. Standing crop data, dominant species.^a

Species ^b	19 Apr.	28 June	29 July	22 Aug.	30 Dec. ^c
TSA ^e live	0	549 ± 114	1190 ± 122	695 ± 64	0
dead	0	66 ± 21	0	318 ± 46	237 ± 24
pred.	316				
DSA live	0	300 ± 15	408 ± 19	339 ± 25	0
dead	367 ± 21	314 ± 19	252 ± 20	226 ± 32	378 ± 42
pred.	264				
SP live	0	335 ± 28	452 ± 72	555 ± 46	0
dead	747 ± 37	677 ± 54	502 ± 97	760 ± 79	529 ± 102
pred.	953				
DS live	0	299 ± 28	463 ± 30	381 ± 50	0
dead	370 ± 19	664 ± 42	467 ± 65	475 ± 29	523 ± 48
pred.	401				
JG live	^f	323 ± 48	293 ± 24	236 ± 60	0
dead	240 ± 37	187 ± 44	198 ± 22	271 ± 27	355 ± 16
pred.	321				
SE live	0	124 ± 15	189 ± 32	207 ± 26	0
dead	142 ± 21	57 ± 20	47 ± 9	38 ± 9	134 ± 11
pred.	158				

^a Mean ± ISEM, gms. ash-free dry-weight m⁻².

^b TSA, DSA: tall and dwarf *Spartina alterniflora*; SP: *S. patens*; DS: *Distichlis spicata*; JG: *Juncus Gerardi*; SE: *Salicornia europaea*.

^c Presence of ice on this date resulted in incomplete collections and underestimates of all but JG and DS.

^d Predicted dead standing crop based on data of 22 Aug. and Table 3.

^e TSA, DSA and SE production was done in Area C and SP, DS and JG production in Area B.

^f Traces of growth evident; less than 5 gms.

cover of the pond by floating algal mats during the month and NR is the mean nighttime respiration for the appropriate bell-jar, also multiplied by 30 or 31.

Measurements of production and respiration were made on 11 dates spread among the months of June through October, and respiration was also measured once in November and once in January. Percent cover of the floating mat was measured on all these dates and several others as well. Periods for which no measurements were taken have been extrapolated from those closest in time for which production data were taken and those closest in time and in temperature for respiration. Since the pool was frozen and snow covered for much of the period, the months of December through March were not included. The 8 monthly rates thus calculated by the equations above were summed to yield annual production.

Results. The same five plant species account for 88, 85 and 96% of the total ground cover in Areas A, B and C. If pool habitat

is included as producer type then the six types account for 90, 88, and 96% of total marsh area (Table 1).

Mean elevation decreases slightly from Area A to C as evidenced by proportional increases in *Spartina alterniflora*, especially its tall form which only occurs lower than from 5-10 cm below mean high tide (Chapman 1940; Miller and Egler 1950).

The mean values and standard errors for live and dead standing crops for each of the dominants on 5 dates are given in Table 2. Tall *Spartina alterniflora* has the greatest live standing crop, followed by *S. patens*, *Distichlis spicata*, dwarf *S. alterniflora*, *Juncus Gerardi* and *Salicornia europaea*. *S. patens* supports the greatest combined standing crop due partly to slow decomposition (Blum 1968) and partly to its high rate of production while *Juncus* and *Salicornia* have the lowest standing crops.

The values of 30 Dec. are somewhat low because ice interfered with collections of all except *Distichlis* and *Juncus*. The values of 19 April actually represent the end of the cycle but are used to estimate the probable

dead cover at the beginning of the cycle as well. No growth appeared by 19 April except a trace of *Juncus* (which also reaches its peak live standing crop earliest, and seeds earliest). The other species first show emergent growth near the beginning of May. *Spartina patens* and *Salicornia* reached their peak live standing crops latest (22 Aug.). *S. patens* maintained patches of apparently live culms under frosted dead cover as late as 30 Dec. The late peak standing crop of *S. patens* may be due to its maintenance of a large dead mat which keeps the soil cold underneath and which also makes it a difficult species to invade and displace (Blum 1968). The late peak of *Salicornia* is probably due in part to the fact that we sampled high panne and drift-line populations, such distributions being characteristic of this marsh. Water-edge *Salicornia* appears to peak earlier and to grow larger but we lack data on this. Our observations suggest that *Salicornia* spp are more important on the sandy Cape Cod marshes than they are at Parker River.

As part of our calculations of emergent production we estimate the amount of dead material expected to be lost to export or decomposition during a sampling interval. This estimate is made from the rates of loss of dwarf *S. alterniflora* dry-weight from litterbags which were originally placed in September, and sampled for two years. Table 3 gives the loss data averaged from replicate samples at 4 locations after different times have elapsed (details in Montagna and Ruber 1980). The most useful rates to our calculations are the interpolated rates

for 19 April–28 June (15.8%), 1 May–28 June (14.3%), 28 June–29 July (16.7%), 28 June–22 Aug. (23.5%), 29 July–22 Aug. (12.6%), 1 Sept.–19 April (43%), and 1 Sept.–19 April after the lapse of an additional year (85%).

The last two values (43% and 85%) are used to predict the remaining standing crop on 19 April from cumulative losses of 2 years based on the crops of 22 Aug. (Table 2). The comparisons of observed with expected standing crop show differences of from 10–30%, not surprising considering the variables of time, site and species. Except for dwarf *S. alterniflora* the 19 April dead standing crops were lower than predicted, probably because the protection of the litterbags in the field experiments reduced losses below what would normally occur free on the marsh. Predicted values for the April dead standing crop of tall *S. alterniflora* are given but were not relevant to actual events since ice sheared-off all of this ecophene to almost mean high tide levels, where it grades into the intermediate sized form. The December data were not used because the presence of ice made us doubt the completeness of collection.

A sample calculation of annual net primary production is shown for *Distichlis spicata* (Table 4), yielding a value of 898 gms. ash-free dry weight $m^{-2} yr^{-1}$ or assuming a 4.65 kcal to gm. conversion (Gabriel and de la Cruz 1974) 4176 kcal $m^{-2} yr^{-1}$. The value for loss to export or decomposition during an interval is obtained by $(D_n + D_{n+1})/2$. (loss rate from Table 3). In this way the other productivities were calculated, and are presented in Table 7.

Table 3. Losses of dwarf *Spartina alterniflora* dry-weight from litterbags collected from the field for a 19-month period.^a

Month	S	O	N	D	J	F	M
Months elapsed	0	1	2	3	4	5	6
% remaining	100	82	70	64	62	60	58
% loss rate ^b		18.0	9.8	8.6	3.2	3.2	3.3
Month	A	M	J	J	A	S...M	
Months elapsed	7	8	9	10	11	12	19
% remaining	56	54	48	42	35	28	15
% loss rate ^b	3.4	3.6	11.1	12.5	16.7	20.0	46.0

^a Details in Montagna and Ruber 1980.

^b Normalized % rate beginning with the previous month in the table.

Table 4. Production calculations for *Distichlis spicata*.

Date	Live (L)	ΔL	Dead (D)	ΔD	De + E ^a	H	SUM
19 April	0	299	370	294	82		675
28 June	299	164	664	-197	94		164
29 July	463	-82	467	8	59		0
22 August	381	-381	475	120	334		0
30 December	0		355				—
							839
						59 ^b	59
							—
							898

^a Litterbag estimates from rates in Table 3, assuming rates of decomposition for dwarf *S. alterniflora* can be extrapolated to other species. Rates of production ignoring this factor can be found in Table 7.

^b Losses to herbivores assumed to be 7% of annual crop (Smalley 1959).

Production in pools is calculated in Table 5 in which the monthly production of each sub-community is given and summed. Table values are in grams O₂ m⁻² and are converted to a value comparable with that of the emergents by:

$$\frac{\text{gms O}_2 \frac{30}{32}}{1.2} = \text{gms ash-free dry weight}$$

where 30/32 converts to molecular weight of CH₂O and the photosynthetic quotient of 1.2 is assumed (Strickland and Parsons 1960). Thus the value of 514 gms. ash-free dry-weight m⁻² yr⁻¹ (or about 2500 Kcals) is obtained. Plankton algae (dominated by diatoms and dinoflagellates) contributed the most because of their consistency. The production from the floating mat (mainly

Cladophora sp.) was very great, but limited by the variable proportion of cover by this form (Table 5, Column C). Spring high tides sometimes sweep these mats completely out of a pool leaving the *Cladophora* stranded, to die and slowly decompose, among the nearby grasses. The benthic mat was dominated by blue-greens which showed the greatest potential for production in the warmest months, but which were limited by shading from the floating mat cover. Emergent and pool production values are integrated with percentage cover so that the weighted production for each area can be calculated (Table 6). We obtain for areas A, B and C, the values 614 ± 78, 642 ± 38 and 706 ± 65 gms ash-free dry weight m⁻² yr⁻¹ respectively. While these differences are not sta-

Table 5. Net primary production of three pool communities.^a

Month	Plankton		Floating Mat			Benthic Mat		Total DNP	Total NR	Total 24 hr. NP
	DNP ^b	NR ^c	DNP	NR	C ^d	DNP	NR			
April	81.7	6.4	1.7	0.3	3	34.0	12.7	117.4	19.4	98.0
May	81.8	14.6	3.5	0.7	6	34.0	13.4	119.3	28.7	90.6
June	101.7	16.0	2.9	0.7	5	33.3	16.9	137.9	33.6	104.3
July	33.4	28.0	95.2	9.7	42	39.3	11.9	167.9	49.6	118.3
Aug.	30.5	26.2	55.4	9.7	31	91.0	17.8	176.9	53.7	123.2
Sept.	34.6	43.3	50.6	21.4	42	13.7	18.9	98.9	83.6	15.3
Oct.	51.2	12.1	21.1	3.3	17	29.3	5.5	101.6	20.9	80.7
Nov.	14.2	0 ^e	—	—	0	13.3	0 ^e	27.5		27.5
Total	429.1	146.6	230.4	45.8		287.9	97.1	947.4	289.5	657.9

^a Grams O₂ m⁻².

^b Daytime net production for the month.

^c Night respiration for the month.

^d % area of pond covered by the floating mat.

^e Probably not zero but not measureable over a period of several hours.

Table 6. Net primary production of three marsh areas.

Species ^a	Production P ^b	Area A		Area B		Area C	
		C ^c	PC ^d	C	PC	C	PC
TSA	1256	0.0	0	4.9	62	7.0	88
DSA	408	6.4	26	16.0	65	24.9	102
SP	813	25.5	207	19.9	162	45.6	371
DS	757	17.2	130	29.4	223	8.8	67
JG	339	3.3	11	12.1	41	0.4	1
SE	207	1.2	2	2.8	6	0.5	1
Pools	514	<u>26.0</u>	<u>134</u>	<u>0.0</u>	<u>0</u>	<u>8.3</u>	<u>43</u>
		79.6	510	85.1	559	95.5	673
Others		20.4	<u>104^e</u>	14.9	<u>83</u>	4.5	<u>33</u>
			614		642		706
			(78) ^f		(38)		(65)

^a Species abbreviations keyed in footnote to Table 2.

^b Production in gms. ash-free dry weight m⁻² yr⁻¹.

^c Percent relative cover values.

^d Relative production weighted according to cover.

^e Production of other species assumed proportional to dominants.

^f 1 Standard error of mean, extrapolated from errors of the dominants.

tistically significant, the totals are actually built out of very different distributions and productivities of the dominants and we feel that the increase has a real basis.

Discussion. The Rowley Marsh is floristically impoverished even beyond most salt marshes; many forbs common to other marshes in the region are missing. The marsh is quite mature, with little tall *S. alterniflora*, and has a long history of human use in haying and in mosquito control in the course of which many drainage channels were dug and numbers of circular ponds were created by explosions. These activities have largely stopped but their effects remain. Successional events combined with sub-habitats eliminated by human actions possibly have resulted in this loss of minor species.

Our values for the production of tall *S. alterniflora* fall close to those of Squiers and Good (1974) for New Jersey and Wass and Wright (as cited in Keefe 1972) for Virginia, are considerably below (less than half) those of Odum and Fanning (1973) in Georgia, and considerably above those of Hatcher and Mann (1975) in Nova Scotia. Production of the dwarf ecophene of *S. alterniflora* is about 20% lower than N.J. (Squiers and Good 1974). The production of *S. patens* and *D. spicata* is considerably

above previous N.J. and Virginia values. It should be noted that assumptions regarding losses to decomposition and or export play a large role in this and that calculations of decomposition for various plants based on experiments with dwarf *S. alterniflora* may not be valid. Consequently, we have omitted these calculations in the data used for Table 6, and have presented the production data calculated from several assumptions in Table 7. Our values for *J. Gerardi* are nearly twice those for above ground production in the Baltic meadows (Tyler 1971). We have not found sources to compare with our values for *Salicornia europaea*, *Typha angustifolia* or *Scirpus olneyi*.

Within our sample intervals we have not treated the figures as though changes were on a continuum. Our observations suggest that export, if it occurs, is likely to be tied to peak tidal events. On the dry high-marsh areas, decomposition rates are probably at their highest after such tides as well, and therefore, abrupt rate changes are likely to occur.

Net pool production of 514 gms. ash-free dry-weight m⁻² yr⁻¹ (193 gms. carbon) is quite comparable with Pomeroy's (1959) 180 gms. C in Georgia on intertidal mudflats and Gallagher and Daiber's (1974) values of 160 gms. C on marsh surfaces in Delaware but exceed considerably Leach's

(1970) values of 62 gms. C on a British intertidal mudflat.

Hatcher and Mann (1975) did not find evidence of latitudinal difference in overall marsh production. Mendelssohn and Marcellus (1976), finding distinct variation within a relatively small area in Virginia, suggested salinity, nitrogen and phosphorus as likely limiting factors while Nixon and Oviatt (1973) in Rhode Island found ammonia nitrogen significantly correlated with standing crop. Proximity to tidal water affects *S. patens* growth (Blum 1968) and *S. alterniflora* shows similar patterns in its ecophenes.

Our values for 3 areas fall within the range reviewed by Keefe (1972), and by Mendelssohn and Marcellus (1976). The values reported, however, have a very broad range, production being affected by numerous variables cited above. The development of an energy budget for a marsh requires adequate on-site studies rather than a recourse to the literature.

Literature Cited

- ADAMS, D. 1963. Factors influencing vascular plant zonation in North Carolina marshes. *Ecology* 44: 445-456.
- ANON. 1965. Standard Methods for the Examination of Water and Wastewater. 12th ed. Amer. Public Health Assoc. 769 pp.
- BLUM, J. 1968. Salt marsh *Spartinas* and associated algae. *Ecol. Monogr.* 38 (3): 199-221.
- CHAPMAN, V. J. 1940. Studies in salt marsh ecology. Sections VI and VII. Comparison with the marshes of North America. *Jour. Ecol.* 28: 118-152.
- GABRIEL, B. C. and A. A. DE LA CRUZ. 1974. Species composition, standing stock, and net primary production of a salt marsh community in Mississippi. *Ches. Sci.* 15 (2): 72-77.
- GALLAGHER, J. L. and F. C. DAIBER. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. *Limnol. Oceanogr.* 19 (3): 390-395.
- GILLIS, G. 1977. Energy flow in a harpacticoid community of a salt pool. Ph.D. Diss., Northeastern Univ., Boston, Mass. 201 pp.
- GREIG-SMITH, P. 1964. Quantitative Plant Ecology. 2nd ed. Butterworth. London. 256 pp.
- HATCHER, B. G. and K. H. MANN. 1975. Above-ground production of Marsh Cordgrass (*Spar-*

Table 7. Net primary production calculated in four ways.

Species ^a	Peak Live ^b Alone	+	Dead ^c	+	Decomposition Export ^d	+	Herbivory ^e
TSA	1190 ^f (122) ^g		1256 (124)		1261 (124)		1349 (138)
DSA	408 (19)		408 (19)		409 (56)		438 (61)
SP	555 (46)		813 (106)		935 (141)		1000 (154)
DS	463 30		757 (55)		839 (86)		898 (95)
JG	323 (48)		339 (59)		381 (69)		407 (75)
SE	207 (26)		207 (26)		207 (26)		221 (29)
<i>Typha</i>	530 (130)		—		—		—
<i>Scirpus</i>	341 (31)		—		—		—

^a Abbreviation keys in footnote Table 2.

^b Using only peak live standing crop to calculate this column and adding a factor at a time to calculate the next three columns.

^c These values are used in Table 6.

^d We assume for the purposes of this calculation that decomposition values obtained for drawf *S. alterniflora* can be extrapolated to the other species.

^e Using Smalley's value of 7% and assigning an SEM of 3%.

^f Values in gms ash-free dry-weight m⁻² yr⁻¹.

^g Values in parentheses are 1 Standard Error of Mean.

- tina alterniflora*) near the northern end of its range. Jour. Fish. Res. Bd. Can. 32: 83-87.
- HINDE, H. P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide levels. Ecol. Monogr. 24 (2): 209-225.
- KEEFE, C. 1972. Marsh production: A summary of the literature. Contr. Mar. Sci. 16: 163-181.
- KIRBY, C. J. and J. G. GOSSELINK. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. Ecology 57: 1052-1059.
- LEACH, J. H. 1970. Epibenthic algal production in an intertidal algal mud flat. Limnol. Oceanogr. 15: 514-521.
- MENDELSSOHN, I. A. and K. L. MARCELLUS. 1976. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. Ches. Sci. 17 (1): 15-23.
- MILLER, W. R. and F. E. EGLER. 1950. Vegetation of the Wequetequock-Pawcatuk tidal marshes, Connecticut. Ecol. Monogr. 20: 143-171.
- MONTAGNA, P. A. 1975. Rates of decomposition of *Spartina alterniflora* and the occurrence of associated organisms in a Massachusetts salt marsh. M.S. Diss., Northeastern Univ., Boston, Mass. 110 pp.
- and E. RUBER. 1980. Decomposition of *Spartina alterniflora* in different seasons and habitats of a Northern Massachusetts salt marsh, and a comparison with other Atlantic Regions. Estuaries 3(1): 61-64.
- MURRAY, R. E. 1978. Detrital standing crop and flux in a New England salt marsh. M.S. Thesis, Northeastern Univ., Boston, Mass. 106 pp.
- NIXON, S. W. and C. S. OVIATT. 1973. Analysis of variation in local standing crop. of *Spartina alterniflora*. Bot. Mar. 16: 103-109.
- ODUM, E. P. and A. A. DE LA CRUZ, 1967. Particulate organic detritus in a Georgia salt marsh. In: G. Lauff (Editor), Estuaries. A.A.A.S., Washington, D.C. pp. 383-388.
- and M. E. FANNING. 1973. Comparison of productivity of *Spartina alterniflora* and *Spartina cynosuroides* in Georgia coastal marshes. Bull. Georgia Acad. Sci. 31: 1-12.
- POMEROY, L. R. 1959. Algal productivity in the salt marshes of Georgia. Limol. Oceanogr. 4: 386-397.
- RANWELL, D. S. 1974. The salt marsh to tidal woodland transition. Hydrobiol. Bull. 8 (½): 139-151.
- SMALLEY, A. E. 1959. The growth cycle of *Spartina* and its relation to insect populations in the marsh. In: Proc. Salt Marsh Conf. Mar. Inst. Univ. Georgia. pp. 96-97.
- SQUIERS, E. R. and R. E. GOOD. 1974. Seasonal changes in productivity, caloric content, and chemical composition of a population of salt marsh cord-grass (*Spartina alterniflora*). Ches. Sci., 15 (2): 63-71.
- STRICKLAND, J. D. H. and T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Bd. Can., 167: 311 pp.
- TYLER, G. 1971. Distribution and turnover of organic matter and minerals in a shore meadow ecosystem, studies in the ecology of Baltic sea-shore meadows V. Oikos 22: 265-291.
- VADAS, R. L., M. KESER, P. C. RUSANOWSKI, and B. R. LARSEN. 1976. The effects of thermal loading on the growth and ecology of a northern population of *Spartina alterniflora*. In: Esch and McFarlane (eds.) Thermal Ecology II. ERDA Symp. Ser. Conf. 750425, Augusta, Georgia. pp. 54-63.
- VALIELA, I., J. M. TEAL and W. SASS. 1975. Production and dynamics of salt marsh vegetation and the effect of experimental treatment with sewage sludge: biomass, production and species composition. Jour. Appl. Ecol. 5: 477-481.
- WILEY, M. (ed). 1976. Estuarine Processes. Vol. II. Acad. Press., N.Y. 428 p.