Export of detritus from eelgrass (*Zostera marina*) beds near Beaufort, North Carolina, USA

Steven D. Bach¹, Gordon W. Thayer² & Michael W. LaCroix²

¹ WAPORA, Inc., 5980 Unity Drive, Suite F, Norcross, Georgia 30071, USA

² National Marine Fisheries Service, Southeast Fisheries Center, Beaufort, North Carolina 28516, USA

ABSTRACT: Eelgrass *Zostera marina* and shoalgrass *Halodule wrightii* occupy about 93 km² within the 532 km² estuarine system near Beaufort, North Carolina, but account for a major portion of total primary production. To estimate exchange with adjacent areas, we measured export of detritus (including live and dead seagrass blades, roots and rhizomes, macroalgal fronds, *Spartina alterniflora* stems, and particulate organic matter) from 2 sheltered embayment-type grass beds and an open water bed. We also estimated export from a much larger part of the estuary (Bogue Sound). Rates of export of *Z. marina* detritus from an embayment-type bed at Phillips Island ranged from 4.9 to 6.0 g ash-free dry weight mo⁻¹ m⁻² during summer 1976, equivalent to a total of 195 to 240 kg mo⁻¹ for the bed, or to 456 to 558 metric tons mo⁻¹ for the 532 km² estuary, assuming seagrasses cover 93 km². Rates of export of *Z. marina* from the Harkers Island (exposed) and Middle Marsh (embayment) beds were 13 and 1 g afdw mo⁻¹ m⁻², respectively, equivalent to 1200 and 112 t mo⁻¹ for the whole estuary. These differences in export between embayment and open water types of seagrass beds are due to entrapment of floating detritus by embayment beds. The amount of detrital material exported from Bogue Sound was an extremely small portion of the total estimated biomass, due to influences of basin shape. When total amounts of material exported are compared with other sources it can be concluded that seagrass beds contribute important amounts of detrital material to the carbon cycle of this estuary.

INTRODUCTION

The seagrass *Zostera marina* (eelgrass) is a widespread and important primary producer in shallow nearshore marine environments of the United States and elsewhere (Thayer et al. 1984, Zieman 1975, McRoy & Helfferich 1977). Plant material produced in eelgrass beds is contributed by seagrasses themselves (*Zostera marina* or *Halodule wrightii*) and by other primary producers such as phytoplankton, benthic macroalgae and epiphytic algae. A portion of the plant material produced within an eelgrass bed may be retained and recycled in the sediments. A portion may also be exported in the form of blades, particulate organic matter (POM), or dissolved organic matter (DOM). Detrital material exported to adjacent unvegetated areas may serve an important ecological role by providing a source of nutrition for microbes and larger detritivores. However, although the production ecology of eelgrass (Penhale 1977, Thayer et al. 1984) and various aspects of eelgrass decomposition have been studied (Josselyn & Mathieson 1980, Kenworthy &

Thayer 1984), little is known concerning the types and relative amount of detrital material exported (Thayer et al. 1975a, Thayer et al. 1984).

Quantitative studies of export of detrital material in coastal areas have been limited largely to *Spartina alterniflora* (Nixon 1980) even though the importance of detritus in these systems was hypothesized over 60 yr ago (Petersen & Boysen-Jensen 1911, Petersen 1918). Early workers provided qualitative evidence of the importance of detritus exported from European *Zostera marina* beds (Ostenfeld 1908, Blegvad 1914, Petersen 1918). In the United States, studies of seagrass export have also been primarily qualitative. Marshall (1970) estimated that about 2/3 to 3/4 of the annual production in New England *Zostera marina* beds was recycled into sediments. Menzies et al. (1967), Menzies & Rowe (1969) and Wolff (1976) provided qualitative estimates of standing crop and abundance of turtlegrass (*Thalassia testudinum*) blades transported to deep sea areas off the coast of North Carolina. Zieman et al. (1979) quantitatively measured rates of export of blade material from Caribbean seagrass beds. Gallagher et

al. (1984) studied the amounts and types of *Zostera marina* and *Z. japonica* detritus contributed to Oregon salt marshes. The study included estimates of seasonal amounts of detritus in the marsh, variation in rates of eelgrass detritus decomposition, detrital 'community' respiration rates, release and export of DOC, import rates of macrodetritus and nutrient input rates. Other than the studies by Zieman et al. (1979) and Gallagher et al. (1984) no quantitative measurements of export from seagrass beds have yet been made. The overall objective of the present study was therefore to make quantitative measurements of rates of detrital export from eelgrass beds in order to identify the types of material exported and the primary factors controlling rates of export.

The present study was conducted in the 532 km² estuary near Beaufort, North Carolina (USA). The area includes the North and Newport River estuaries (Fig. 1). *Zostera marina* has been estimated to account for approximately 64 % of the total primary production in this estuary (Thayer et al. 1975a, Penhale & Smith 1977). Approximately 55 % of the total production by phytoplankton, benthic algae, and *Z. marina* in a New-

port River eelgrass bed was estimated to be consumed by macrofauna (Thayer et al. 1975b). The remaining portion was available either for consumption by meiofauna, microfauna and microbes, for sedimentation, or for export to surrounding areas. In the present study, it was hypothesized that a large portion of the eelgrass produced could be exported as detritus, which could play an important trophic role in unvegetated areas. Benthic macroalgae, other seagrasses such as *Halodule wrightii* and microalgae were also identified as possible important sources of detritus.

The specific objectives of the present study were to estimate the amounts of detritus exported by eelgrass beds in the study area, to determine the major factors which controlled export, and to compare the rates of export with other sources of detritus. These objectives were achieved by: (1) estimating seasonal patterns and relative amounts of eelgrass and other plant material exported from a sheltered embayment bed (Phillips Island); (2) estimating and comparing rates of export of eelgrass and other plant material from an embayment type bed (Middle Marsh) and an open bed (Harkers Island); (3) measuring rates of export of eelgrass and

Fig. 1 The eastern North Carolina shoreline showing location of study area near Beaufort, and sites where measurements were made: (1) Drum Shoals (biomass stations for Bogue Sound); (2) Atlantic Beach Causeway Bridge; (3) Phillips Island eelgrass bed; (4) Middle Marsh eelgrass bed; (5) Harkers Island eelgrass bed

other plant material from a larger portion of the estuary (Bogue Sound); and (4) comparing the results to previous studies and to estimated amounts of export by other primary producers in the study area.

MATERIAL AND METHODS

Seasonality of export was examined by making weekly measurements of surface-drifting plant material in an eelgrass bed at Phillips Island (Fig. 1). Surface-drifting plant material was collected in floating nets ($1.0 \times 0.3 \times 0.3$ m) (Fig. 2) placed at each end of the eelgrass bed across the main axis of tidal flow (Fig. 3). Four nets (two 500 μ m and two 250 μ m mesh) were set at each end of the grass bed, and plant material was collected over a known portion of the tidal cycle. The 250 μ m nets were used to collect particulate organic matter (POM). Net export rates were estimated by subtracting mean amounts of plant material caught in the inflow and outflow nets and extrapolating this value to the entire tide cycle.

Rates of export were initially expressed as mg dry weight of plant materials per m^3 of water that passed through the nets. Water volumes were estimated by measuring current velocities simultaneously during each collection period with one TSK flowmeter (model WA-200) placed next to each set of nets. The meters were calibrated to correct for effects of backwash produced by resistance of the collecting nets to flow. A net backwash factor was determined by measuring the difference between current readings of meters inside and outside net openings over a range of current velocities. Export rates in mg dry wt m^{-3} were corrected

for backwash and then converted to $\text{mg dry wt m}^{-3} \text{ tide}^{-1}$ by extrapolation to the full tidal cycle (for the top 0.3 m of water column only). This was done by dividing values of export in mg dry wt m^{-3} by the percentage of the total tidal volume sampled. The method assumes that the material in the upper 0.3 m is representative of the whole water column (total height of the water column was less than 1 m in both study areas).

Total tidal volume was estimated by making separate measurements of current velocities over a single complete flood and ebb tide cycle and calculating the sample period as a percentage of the total area under the tidal velocity curve (about 60 % of the tidal cycle was sampled). Values in $\text{mg dry wt m}^{-3} \text{ tide}^{-1}$ were multiplied by the estimated total discharge across the upper 0.3 m of the water column over the bed (the depth of the nets) to give $\text{mg dry wt tide}^{-1}$. Discharge was determined separately each sampling day by combining information on tidal velocities and tabulated values of predicted tide heights. Daily rates of export were based on 4 tides d^{-1} and monthly rates were estimated by multiplying daily rates by the number of days in the month. Final values were expressed in g ash-free dry wt (afdw) based on organic content of pooled samples for each collection. Organic content was determined by measuring weight loss of dried material at 550 $^{\circ}\text{C}$.

From July to December 1976, export was measured by using 4 freely swinging nets. Each was loosely attached to a vertical steel pole by a 'U' bolt to allow for free horizontal and vertical movement. However, strong winds occasionally turned some of the nets around, so that after December 1976, 2 of the nets in

Fig. 2. Nitex mesh nets used to collect drifting plant material

Fig 3. (a) Middle Marsh eelgrass bed. This bed is protected on 3 sides by *Spartina alterniflora* marsh (S), and connected to the rest of the estuary by channels and a shoal on the southern side. The bed is divided into 2 approximately equal halves – the northern half being deeper with fine clay/silt sediments and very dense *Zostera marina* (Z), and the southern half characterized by an elevated shoal of much coarser well-sorted sediments and covered almost entirely by *Halodule wrightii* (H). Solid circles show positions of nets used to collect plant material being imported or exported; arrows denote observed current flows once the shoal is covered with water. (b) Harkers Island eelgrass bed. This bed is located in open water. Outline of bed determined from aerial photographs. Channels are located on all 3 sides of the bed, which is situated on a shoal just south of Harkers Island. Triangles indicate positions of replicate nets; dots indicate small patches of seagrasses (both *H. wrightii* and *Z. marina*)

each set were held in permanent horizontal position by an aluminum frame (with free vertical movement). Material collected by fixed nets represented tidally driven export, while material collected by freely swinging nets represented wind driven export on days when wind velocities were sufficient to reverse the position of the nets. On most days, material was collected twice daily, once on ebb and once on flood tide.

Plant material was returned to the laboratory, rinsed in fresh water and frozen before sorting into fractions and weighing. Fractions included live (green) and dead (brown) *Zostera marina* blades and rhizomes; *Halodule wrightii* blades, rhizomes, and roots (pooled as 1 fraction); *Spartina alterniflora* stems and leaves; macroalgae; and particulate organic matter (POM) (from the 250 μ m nets).

The effect of bed type on export rates was determined by making measurements in 2 different kinds of eelgrass beds (open versus embayment) in the North River estuary (Fig. 3). These are the 2 primary types of seagrass beds present in this estuary, and represent the range of hydrologic conditions which might affect export. The open eelgrass bed was located just south of Harkers Island in open water, several hundred meters from the nearest land or *Spartina alterniflora* marsh. The eelgrass bed at Middle Marsh was enclosed on 3 sides by *S. alterniflora* and connected to the adjacent estuary by 4 channels and a large opening across a shoal area (Fig. 3). Detritus was sampled by collecting surface drifting material in replicate nets placed on the inflow and outflow sides of each bed (Fig. 3). The amount of bottom-drifting plant material was measured at these 2 locations during summer 1978 by positioning nets without floats on the bottom.

To measure export from a larger portion of the estuary, drifting plant material from Bogue Sound was collected under the Atlantic Beach causeway bridge (Fig. 1 & 4) on ebb and flood tides. Nine nets were attached to 10 m lines at known intervals along the bridge. Export was extrapolated from the difference in mean amounts of plant material caught on ebb and flood tides for all sampling days (samples were taken on 14 dates between 26 July and 25 August, 1977).

For all study sites, export was also expressed as a percentage of biomass and production. Biomass data were obtained using stratified random sampling. All biomass samples were collected between June and August during 1976 (Phillips Island), 1977 (Bogue Sound) and 1978 (Harkers Island and Middle Marsh) (Fig. 1). Peak biomass for *Zostera marina* typically occurs between March and June in this estuary, whereas *Halodule wrightii* typically reaches its peak biomass in August–September. Between 20 and 45 samples were taken in each bed with a 14 cm diameter post hole digger. Total biomass for the eastern part of Bogue Sound was estimated from data given in Dillon (1971). Additional data on biomass were taken from Thayer et al. (1975b) and Penhale & Smith (1977). To determine total biomass of Harkers Island and Middle Marsh eelgrass beds, biomass estimates for each bed were combined with estimates of horizontal extent made from aerial photographs.

Leaf production was measured using a technique

Fig. 4. Location of eelgrass beds in Bogue Sound at which biomass samples were collected during summer of 1977. Numbers denote approximate location of each bed

described by Kenworthy (1981). This is an indirect method based on measurements of the time interval between leaf scars (plastichromes) on the seagrass rhizome and the known weight of individual leaves of various ages measured from biomass samples.

Leaf production in $\text{dry wt m}^{-2} \text{d}^{-1}$ was estimated by multiplying shoot production by density of shoots (no. m^{-2}). Shoot density was determined from random samples of biomass collected in each eelgrass bed. Kenworthy (1981) provides further details concerning all aspects of this method of estimating production.

RESULTS

Phillips Island

The majority of surface-drifting plant material exported from the Phillips Island eelgrass bed consisted of complete or partially complete green *Zostera marina* blades with dead (brown) tips and epiphytes still attached. Complete shoots with rhizomes, roots, and blades were also collected but in much smaller amounts. Of the total amount of *Z. marina* collected during summer (the period of maximal export), approximately 65 % was live, 33 % was dead (brown), and 2 % was rhizome. The macroalgal fraction primarily consisted of living fragments of *Sargassum*, *Ectocarpus*, and *Aghardiella* spp. The *Spartina alterniflora* fraction consisted almost entirely of dead portions of mature stems or rhizomes.

Maximum *Zostera marina* export rates of 195 to 240 kg afdw mo^{-1} were followed by a rapid reduction in

Fig. 5. Rates of export of surface drifting plant detritus (in kg afdw mo^{-1}) estimated to occur at the Phillips Island eelgrass bed during 1976–1977. Each point represents mean kg mo^{-1} exported based on observed daily rates ($n = 8$ to 20 for each point)

export during September and October and low export rates from November 1976 to August 1977 (Fig. 5). The reduction in September was accompanied by a major drop in *Z. marina* biomass, which continued through August 1978 (based on visual observations of blade loss plus aerial photographs of the bed). Analysis of variance showed a significant net export (as g afdw tide⁻¹) on 64 % of the days sampled between July 1976 and February 1977. Since *Z. marina* biomass had decreased greatly by February 1977, no significant net export occurred on 77 % of the days sampled from March to September 1977 ($p=0.05$ in all tests).

Since net export was calculated from the difference in mean amounts of material caught in the import and export nets, it was not possible to calculate a standard deviation for this estimate. However, standard deviations and co-efficients of variation were calculated for mean amounts of 'Total *Zostera marina*' (leaves, roots and rhizome sub-fractions), in order to provide an estimate of the variation in amounts of material caught between nets. The grand mean coefficient of variation for 54 d of data (13 Jul 1976 to 15 Feb 1977) for the import nets was $106 \pm 47\%$. The grand mean coefficient of variation of material caught in the export nets was $56 \pm 31\%$. A graph was also constructed which showed the cumulative mean coefficient of variation versus increasing number of samples collected. After about 20 data points, the amount of variation in the cumulative mean coefficient became greatly reduced. The same reduction in variation occurred after about 30 sampling points for the import nets. This analysis provides some idea of the amount of between-net variation involved.

The amount of *Zostera marina* exported during July and August 1976 ranged from 7.3 to 9.0 % of the total aboveground biomass and production in the bed. The mean aboveground biomass in July and August was

66.48 ± 38.41 g afdw m⁻² in the 40,000 m² area covered by eelgrass, yielding a total biomass for the Phillips Island bed of 2.66×10^3 kg afdw. The percent exported in July, therefore, was $(195 \text{ kg}/2.66 \times 10^3) \times 100 = 7.3\%$, and in August (240 kg) was 9.0 %. However, these values could possibly range from 1 to 20 % based on the observed variations in export and biomass. Similarly, if 2.63 g afdw m⁻² d⁻¹ is the assumed production of *Z. marina* in July and August (Penhale 1977), total production per month would average 3156 kg afdw (i.e. $2.63 \text{ g afdw m}^{-2} \text{ d}^{-1} \times 40,000 \text{ m}^2 \times 30 \text{ d}$). This indicates that 6 to 8 % of the production was exported per month during July and August 1976.

Movement of *Zostera marina* was affected significantly by wind, as observed on several days when wind caused surface-drifting plant material to be transported in the direction opposite tidal flow. For example, during the afternoon of 18 August 1976, a 50 to 60 km h⁻¹ wind from the NE produced surface transport of 2.2 kg afdw of *Z. marina* in the opposite direction to the flooding tide. That morning the wind had been in the same direction as the tide and 3.9 kg of *Z. marina* were exported with the tide. Similar effects were observed on 7 other days with winds of approximately the same strength.

The seasonal pattern of export of macroalgae and *Spartina alterniflora* from the Phillips Island bed is summarized in Fig. 5. During August and September 1976, import of *S. alterniflora* and macroalgae (primarily *Sargassum* spp.) was observed, followed by net export of macroalgae (*Gracilaria*, *Dictyota*, *Aghardiella* spp.) and *S. alterniflora* from October to January, and import of the brown alga *Ectocarpus* spp. in February. The following spring and summer, net export of *S. alterniflora* and macroalgae was observed. Total material exported ranged from 4 to 36 kg afdw mo⁻¹,

Table 1. *Zostera marina*. Comparison of biomass and production with export from Harkers Island and Middle Marsh beds in 1978 (negative sign indicates import)

	Biomass* (kg)	Export (kg mo ⁻¹)	Export as % of biomass	Production** (kg mo ⁻¹)	Monthly export as % of monthly production
Harkers Island					
Jun	6774	2184	32	7050	30
Jul	7736	934	12		13
Aug	2209	722	33		10
Middle Marsh					
Jun	5746	-9.9	-0.2	3180	-
Jul	5469	78	1.4		2.5
Aug	1188	30	2.5		0.9
* Of entire bed (afdw)					
** Mean rate of leaf production of whole bed for June, July and August (afdw)

Fig. 6. Comparison of export at Harkers Island and Middle Marsh beds during summer 1978. Mean monthly values are based on daily rates for 6 to 10 d per bed for the summer. Z = *Zostera marina*; H = *Halodule wrightii*; M = macroalgae/*Spartina alterniflora* fraction

while that imported ranged from 1 to 41 kg afdw mo^{-1} (Fig. 5). Analysis of variance showed that export of these materials was statistically significant on 64 % of all days sampled ($p = 0.05$ in all tests). A Student-Newman-Keuls (SNK) test showed no statistical differences in magnitude of total material exported between months. The lack of differences was attributed to the

large amount of variation in material caught between replicate nets.

Export of POM from Phillips Island ranged from 9 to 156 kg afdw mo^{-1} (Fig. 5). Import of approximately 95 kg afdw occurred in January 1977. There was significant net export of POM from the bed on 38 % of the days sampled ($p = 0.05$). However, the SNK test showed no differences in export between the months that were sampled. Evaluation of plankton net material showed that the POM fraction consisted of approximately 10 to 30 % zooplankton during summer but from 90 to 95 % zooplankton in winter.

Middle Marsh and Harkers Island

The analysis of variance showed that except for 2 dates there was statistically significant net export of *Zostera marina* and *Halodule wrightii* from Middle Marsh and Harkers Island. Based on the 6 data sets collected at Harkers Island, net export of *Z. marina* (all fractions) averaged 2184 kg afdw for June, 934 kg for July, and 722 kg for August (Fig. 6; Table 1). Export of *H. wrightii* at Harkers Island followed an opposite pattern, increasing from 116 kg in June to 446 kg in July and 887 kg in August (Fig. 6). This increase was paralleled by a simultaneous increase in *H. wrightii* biomass (Tables 2 & 3). Export of macroalgae from Harkers Island was not significant in June and July, but 1200 kg afdw (primarily as *Ectocarpus*) were exported in July (Fig. 6). Large amounts of *Ectocarpus* spp. were observed within this bed during August.

A slight net import of *Zostera marina* at Middle Marsh occurred in June. Approximately 78 kg afdw was exported in July and 27 kg in August (Fig. 6). The pattern shown by *Halodule wrightii* at Middle Marsh was opposite that at Harkers Island, with 896 kg

Table 2. *Halodule wrightii*. Comparison of biomass and production with export from Harkers Island and Middle Marsh beds in 1978

	Biomass* (kg)	Export (kg mo ⁻¹)	Export as % of biomass	Production** (kg mo ⁻¹)	Monthly export as % of monthly production
Harkers Island					
Jun	313	116	37	4189	2.8
Jul	605	446	74		10.6
Aug	1196	887	74		21.2
Middle Marsh					
Jun	659	112	17	3091	3.6
Jul	1155	27	2		0.9
Aug	713	13	2		0.4
* Of entire bed (afdw)					
** Mean rate of leaf production of whole bed for June, July and August (afdw)					

Table 3. Biomass of *Zostera marina* live (ZL) and dead (ZD) fractions and *Halodule wrightii* (H) at Middle Marsh and Harkers Island during June, July and August, 1978. Values represent aboveground blade biomass in g afdw m⁻²

Date	Fraction	Biomass at Middle Marsh Deep		Biomass at Middle Marsh Lagoon		Biomass at Harkers Island	
		Mean	SE	Mean	SE	Mean	SE
19 Jun 1978	ZL	16.61	14.23	80.07	45.69	43.61	44.09
	ZD	12.07	9.88	42.27	29.05	22.57	20.40
	H	17.58	15.92	0.0		3.06	6.54
19 Jul 1978	ZL	15.48	13.58	68.79	46.60	52.21	39.09
	ZD	11.26	10.95	48.64	39.68	23.36	26.63
	H	30.43	21.59	0.38	2.79	5.91	10.86
31 Aug 1978	ZL	0.98	1.55	16.95	17.09	11.17	12.91
	ZD	1.04	2.37	12.29	14.40	10.40	10.20
	H	19.01	22.17	0.0		11.68	11.69

Table 4. Export of bottom drifting macrodetritus for June, July and August 1978

Fraction	Mean export (kg afdw mo ⁻¹)
Middle Marsh	
Total <i>Zostera marina</i>	3.1
<i>Halodule wrightii</i>	0.3
Macroalgae	-1189.0
<i>Spartina alterniflora</i>	0.5
Harkers Island	
Total <i>Zostera marina</i>	4.5
<i>Halodule wrightii</i>	194.0
Macroalgae*	1574.0
<i>Spartina alterniflora</i>	0
* <i>Ectocarpus</i> spp. (August)	

Table 5. Biomass of *Zostera marina* and *Halodule wrightii* in Bogue Sound, August 1977

Transect	Biomass (g afdw m ⁻² ± 1 SD)	Sample size
<i>Zostera marina</i>		
1	2.40 ± 3.13	17
2	12.80 ± 12.54	14
3	16.89 ± 10.11	17
4	1.95 ± 4.03	12
5	14.66 ± 19.91	21
Grand mean =	9.74	
<i>Halodule wrightii</i>		
1	88.41 ± 72.82	17
2	63.73 ± 55.80	14
3	42.87 ± 49.37	17
4	43.00 ± 49.50	12
5	17.80 ± 23.53	21
Grand mean =	51.15	

exported in June, 27 kg in July and 13 kg in August. From 10 to 50 kg *Spartina alterniflora* and macroalgae were exported each month from the Middle Marsh bed.

Between 10 and 30 % of the *Zostera marina* leaf biomass and production were exported monthly from the Harkers Island bed, while only 0.9 to 2.5 % were exported from the Middle Marsh bed (Tables 1 & 2). Approximately 37 to 74 % of the *Halodule wrightii* biomass was exported from the Harkers Island bed each month, and 2 to 17 % from Middle Marsh (Table 2). Based on rates of production given for this area by Dillon (1971), from 3 to 21 % of the *H. wrightii* production was exported each month at Harkers Island, and 0.4 to 3.6 % at Middle Marsh.

Export of bottom-drifting *Zostera marina* was not substantial at Middle Marsh (Table 4). However, 39.8 kg afdw of macroalgae (*Dictyota* and *Gracilaria* spp.) were imported in June. At Harkers Island, export of bottom-drifting *Z. marina* was also negligible, but 194 kg of *Halodule wrightii* and 1574 kg of *Ectocarpus* were exported in this manner.

Bogue Sound

Biomass of *Zostera marina* along 5 transects in Bogue Sound in August 1977 (Hoop Pole marsh bed) ranged from 1.95 ± 4.03 to 16.89 ± 10.11 g afdw m⁻². The grand mean (n = 81) biomass for all 5 transects was 9.74 g afdw m⁻² (Table 5). Biomass of *Halodule wrightii* along the same 5 transects ranged from 17.80 ± 23.53 to 88.41 ± 72.82 g afdw m⁻² (Table 5).

Mean rates of net export from Bogue Sound (average of net export for all days sampled during July and August 1977) ranged from 11.2 kg mo⁻¹ (for POM) to 150.2 kg mo⁻¹ (for *Halodule wrightii*). About 47.4 kg mo⁻¹ of *Zostera marina*, 31.5 kg mo⁻¹ of macroalgae and 24.5 kg mo⁻¹ of *Spartina alterniflora* were esti-

mated to be exported from Bogue Sound during this same period (Table 6).

On days when the wind blew from the south at sufficient strength, export of drifting seagrass detritus was greatly reduced or even negative (i.e. imported) in Bogue Sound (Table 7). Export of seagrass material from Bogue Sound was much higher on calm days when wind speed was 0 to 5 knots. Export of fractions of other types of detritus was more variable (Table 7).

DISCUSSION

The results of this study illustrate a variety of important aspects regarding the export of plant detritus from eelgrass beds in the North River estuary. These are discussed according to the individual sites at which measurements were made.

Phillips Island

Export rates from Phillips Island varied seasonally and between years. The highest rate of export (240 kg afdw mo⁻¹) occurred in August 1976. Export rates then

dropped sharply through the remainder of 1976 and 1977 (Fig. 5). The maximum rate of export in the summer of 1976 is probably part of the typical seasonal pattern of *Zostera marina* in this estuary because this is the period of greatest temperature-related leaf stress. During low tide, leaves are exposed directly to the sun or are affected by high water temperatures in shallow tidal pools. A portion of the leaves are stressed under these conditions and eventually dehisce. These leaves are removed from the eelgrass bed on subsequent tidal cycles.

The peak biomass of *Zostera marina* in North Carolina typically occurs between March and June (Thayer et al. 1984), but the period of greatest temperature stress is usually in late summer. Therefore, maximum export rates and peak biomass do not necessarily occur at the same time in this system. Export of *Z. marina* leaves should be related in some degree to the rate of leaf turnover (productivity) since under conditions of higher turnover, more leaves are available for removal from the bed. However, this relation was not measured in the present study.

The results at Phillips Island may also reflect a longer term pattern of reduction in biomass caused by

Table 6. Export of surface drifting detritus from Bogue Sound during July and August 1977

Fraction	Mean* ebb (g tide ⁻¹)	Mean* flood (g tide ⁻¹)	Mean net export (g tide ⁻¹) (kg tide ⁻¹ **)		(kg mo ⁻¹)	% of total biomass***
Live <i>Zostera marina</i>	1137.7	694.8	442.9	0.89	26.7	
Dead <i>Zostera marina</i>	397.3	105.9	291.4	0.58	17.4	
<i>Zostera marina</i> rhizomes	72.7	16.6	56.1	0.11	3.4	
Total <i>Zostera marina</i>	1607.7	817.3	790.4	1.58	47.4	.01
<i>Spartina alterniflora</i>	1235.3	827.8	407.5	0.82	24.5	
<i>Halodule wrightii</i>	4114.4	1611.7	2502.7	5.01	150.2	.08
Macroalgae	885.6	360.5	525.1	1.05	31.5	
Particulate** organic matter	2038.7	1852.5	186.2	0.37	11.2	

* Mean afdw values for all days sampled
 ** 2 ebb tides, 2 flood tides
 *** % of total biomass in eastern Bogue Sound estimated to occupy the bottom area covered by the 67 km² tidal prism

Table 7. Comparison of export from Bogue Sound on windy and calm days

Date	Wind (knots)	Net export (g afdw tide ⁻¹) (mean caught in ebb - flood)				
		<i>Zostera marina</i>	<i>Halodule wrightii</i>	<i>Spartina alterniflora</i>	Macroalgae	POM
2 Aug 1977	5-15**	-326.4	-681.4	+1146.6	+212.5	-25.0
10 Aug 1977	15-20**	+154.0	-819.8	-436.3	-86.7	-396.7
18 Aug 1977	0-5	+1910.4*	+3568.8*	+1558.7	+1396.7	+1094.5
25 Aug 1977	0-5	+562.2	+7665.9*	-69.4	+926.2	-323.6

* Significant difference at P = 0.01 level between mean ebb and mean flood values
 ** Wind from south

elevation of the eelgrass bed. Elevation is a result of trapping of sediments by the system of leaves and rhizomes. As the bed builds vertically, plants are exposed increasingly to intertidal conditions (Thayer et al. 1984). This eventually causes dieback, biomass reduction, and therefore, reduced export of blade material. Unusually large reductions in the biomass of *Zostera marina* in late summer at Phillips Island were observed in 2 previous studies (Thayer et al. 1975b, Penhale 1977), which is evidence for a long-term cycle of bed build-up. Such a long-term cycle may have a major effect on export rates in this eelgrass bed.

During winter, significant amounts of export may also occur from the Phillips Island bed, although the data from this study do not support this. Biomass of *Zostera marina* at Phillips Island had been much higher in previous years (Penhale 1977), and during winter in those years, average production rates were never below 50 % of summer rates (Penhale 1977). Rates of export in winter would be expected to be correlated with the amount of leaves present and the rate of turnover of leaf material. It is therefore likely that significant export occurred in winter during those years when biomass was higher. This is another example of the possible effects of the long-term successional cycle of bed elevation mentioned previously.

During July and August 1976, 195 to 240 kg afdw mo^{-1} of *Zostera marina* detritus (exclusive of POM) was exported from the Phillips Island bed. Dividing export values by bed area (40,000 m^2) provides an estimate of 4.9 to 6.0 g afdw mo^{-2} exported. Assuming that export rates for this bed were comparable with other beds in the area at that time and that eelgrass covered 17 % of the 532 km^2 study area (Williams 1973), the amount of *Z. marina* exported to the estuary would have approximated 456 to 558 metric tons mo^{-1} during summer.

Thayer et al. (1975b) estimated that about 45 % of the *Zostera marina* produced in the Phillips' Island bed (3165 kg afdw mo^{-1} during summer) was available for export. If this amount had indeed been exported, it would have equalled approximately 1420 kg mo^{-1} . However, only 6 to 8 % was in fact exported, indicating that the difference, i.e. 1180 to 1225 kg, was available for incorporation into sediments, was cycled within the meadow by bacteria and detritivores, or was available for export as POM or dissolved organic material (DOM).

Because of variability it was not possible to show statistical differences in rates of POM export from Phillips Island between seasons. However, POM quantities could exceed those contributed by surface-floating blade material (Table 6). The large variability of POM export was probably produced by a variety of factors, including seasonal differences in biological

production (i.e. of *Zostera marina*, phytoplankton, and zooplankton), as well as seasonal and spatial variation in winds and currents.

Approximately 65 % of the *Zostera marina* exported in summer from Phillips Island consisted of green (live) blades. Because *Z. marina* decomposes relatively slowly (Harrison & Mann 1975, Thayer et al. 1984), the green leaf material would not be suitable as a food source for detritivores. The blades decompose slowly and reach their optimal nutritional state as detritus only after several months (Thayer et al. 1977). The rate of decay is a function of degree of tidal inundation, temperature, and other local site conditions (Josselyn 1978, Thayer et al. 1984). An immediate role of exported *Z. marina* may therefore not be as a food source but rather as habitat for benthic animals in unvegetated areas. Local fishermen have reported collecting large amounts of *Z. marina* in the deeper portions of Newport River estuary during late summer and early fall, indicating these may be primary sites of accumulation for exported material. Since *Z. marina* is highly epiphytized in late summer (Penhale & Smith 1977), exported plant material may also provide an immediate food source (in the form of its epiphytes) for benthic animals in these same areas.

Since exported *Zostera marina* is not available for several months as a detrital food source, other more readily decomposable plants may serve this function. Macroalgae are composed of more labile components and have more rapid decay rates than *Z. marina* (Tenore 1977, Josselyn 1978). These may serve a more immediate role as detrital food sources. Surface export of macroalgae was highly variable at all locations sampled in the present study. Most of this drifting material appears to leave and enter the seagrass bed along the bottom. Macroalgal export may occur in substantial quantities in this estuary.

Middle Marsh and Harkers Island

The studies at Middle Marsh and Harkers Island illustrate how bed enclosure, intertidal conditions, winds and current interaction, and seasonal changes in plant biomass all affect rates of export in this estuary. Effects of enclosure by salt marshes are indicated by the order of magnitude difference in relative export rates between Harkers Island and Middle Marsh. This difference was probably caused by greater physical retention of detritus in the Middle Marsh bed. Internal processing and recycling of *Zostera marina* blades and other detritus is probably much greater in an enclosed bed such as Middle Marsh. The enclosure of Middle Marsh also reduced the amount of wind scouring of the bottom, thereby reducing detrital suspension. Both

wind and hydrologic conditions thus reduced the total amount of export from this bed.

Temperature measurements over midday during a spring low tide in August 1978 demonstrate an additional effect of bed enclosure. Rapid mid-afternoon rises in water temperature (maximum temperatures of up to 34 °C) were recorded at Middle Marsh, due to reduced current speed and shallow depth, but only a small rise in temperature (+2 °C; up to 30 °C maximum) was noted at Harkers Island because of the faster flow of water. Repeated temperature stress, combined with very low tides and reduced circulation, would be expected to produce leaf mortality and blade loss of *Zostera marina*. This hypothesis is supported by the reduction of *Z. marina* biomass which occurred at Middle Marsh in August 1978 (Table 1). It does not however explain a similar decrease in biomass observed at Harkers Island in August since this bed is located in open water with good circulation. It is possible that blade loss at Harkers Island was related to unusually high late summer temperatures since *Z. marina* is at the extreme southern edge of its range in Beaufort. This could also explain the increase in biomass of *Halodule wrightii* at Harkers Island since this tropical species is at the northern edge of its range in Beaufort and would increase under warmer conditions. An alternative hypothesis could be that over the period of several years the Harkers Island bed has become increasingly elevated due to trapping of sediments by leaves and rhizomes, as may have occurred at Phillips Island. This would expose *Z. marina* to intertidal stress, ultimately producing higher rates of blade loss. Some *Z. marina* beds at Harkers Island were observed to be exposed to such intertidal conditions.

The interaction between wind and tidal currents also has an important effect on export in this estuary. The amount of export was greatest when wind and tide were working in the same direction. Less export resulted when wind and tide worked in opposition. In the present study, wind velocities of over 50 km h⁻¹ were capable of causing transport as high as 0.3 m s⁻¹ against the tidal current. Lower wind velocities would also have some effect but this was not examined further in the present study.

Bogue Sound

The effect of the estuary's shape and physical orientation on export is illustrated by the results of the Bogue Sound study. Bogue Sound is long and narrow and prevailing winds blow across its east-west axis. Larger amounts of surface drifting material wash up on beaches or are carried into deeper channels as wind velocity increases. A significant amount of detritus

from eelgrass beds may also be deposited in *Spartina alterniflora* marshes, and could constitute a detrital input to this system. Other researchers have also reported substantial input of *Zostera marina* detritus to salt marshes (Gallagher et al. 1984). The total amount of seagrass exported from Bogue Sound to adjacent areas, however, was small relative to the total amount of available biomass.

To examine the relative amounts of *Zostera marina* exported from Bogue Sound, rates of export were compared with the total amount of biomass of this seagrass in the Sound. Dillon (1971) estimated that the average biomass of *Z. marina* was 273 g m⁻² in 1966 (based on data from 4 transects) and that this seagrass covered approximately 55 % of the total of the Sound. Since the eastern end of Bogue Sound (the end from which export was measured) is affected by a tidal prism of about 67 km² in horizontal extent it is reasonable to assume that most of the *Z. marina* exported originated primarily from this area. The total biomass of *Z. marina* within the 67 km² tidal prism would therefore roughly equal $0.273 \text{ kg m}^{-2} \times 67 \text{ km}^2 \times 10^6 \text{ m}^2 \text{ km}^{-2} \times 0.55 = 1.01 \times 10^7 \text{ kg}$. Using the results of the summer 1977 sampling, the average biomass of *Z. marina* in the Eastern part of the Sound was determined to be 9.74 g afdw m⁻² (Table 5). Using this as an average for the whole sound, and assuming *Z. marina* still covered 55 % of the bottom, the total biomass would be $0.00974 \text{ kg m}^{-2} \times 67 \text{ km}^2 \times 10^6 \text{ m}^2 \text{ km}^{-2} \times 0.55 = 3.6 \times 10^5 \text{ kg}$. Using either of the above means of estimating biomass, it can be concluded that the amounts of *Z. marina* exported on a monthly basis (47.4 kg mo⁻¹) during summer were an extremely small percentage of the estimated total biomass present within the Sound. This results from retention of the material within the Sound caused by its east-west orientation and the action of wind. Evidence for retention was the commonly observed build-up of seagrass detritus (leaves) on the beaches of the northern side of the Sound. It is not possible to estimate the relative amounts of macroalgae and *Halodule wrightii* exported and/or retained since no recent biomass data are available for the entire Sound. However, amounts exported relative to total biomass are probably also small due to the above factors.

Estimates of the total amount of detrital export for all *Zostera marina* beds in the estuary can be made based on data from Harkers Island and Middle Marsh. This exported material may be transported to other parts of the estuary via tidal channels, where it may accumulate (some detrital material may also be transported to nearshore oceanic waters, but the amounts involved are not yet known). Dividing the mean amounts of *Z. marina* (in kg afdw mo⁻¹) by the areas of each bed yields values of 1.2 and 12.9 g afdw mo⁻¹ m⁻² for these

2 sites, respectively. Multiplying the values for Harkers Island and Middle Marsh by the total area of the estuary occupied by *Z. marina* (93 km²) yields a range of 112 to 1200 metric tons of *Z. marina* exported each month during summer. These values can be compared with the summer Phillips Island estimates, which when extrapolated to the whole estuary yielded a range of 455 to 558 t mo⁻¹ (4.9 to 6.9 g afdw mo⁻²). This is within the same order of magnitude as the estimates made for the Harkers Island and Middle Marsh beds.

Similar estimates for *Halodule wrightii* are more difficult to make because few data on biomass are available. Dillon (1971) reported that *H. wrightii* is capable of rapid horizontal growth. Within 1 yr, it increased from a rare species to cover about 4 % of the bottom of Bogue Sound. Based on measurements by the present author's of *H. wrightii* biomass in Bogue Sound and results of aerial surveys conducted between 1975 and 1978, it can be concluded that *H. wrightii* abundance had increased greatly by 1978. Extensive seagrass beds covering several km² were noted in the summer of 1978 just inside of Core Banks, immediately north of Cape Lookout (Fig. 1) and in other similar areas. Observations made at Core Banks confirmed that these beds were predominantly *H. wrightii*. If *H. wrightii* were to occupy an area equivalent to that of eelgrass in this estuary (93 km²), between 90 and 475 t mo⁻¹ (1.0 to 5.1 g afdw mo⁻¹ m⁻²) could be contributed to the detrital pool during summer.

CONCLUSIONS

The estimates of export made in this paper are affected by several factors, which must be considered in making conclusions concerning the amount of detri-

tal material involved. These factors include: (1) variation in tidal volume discharge estimates; (2) contagious (clumped) distribution of drifting plant material; and (3) long-term change in seagrass abundance and distribution.

Tidal volume discharge varies due to lunar effects and effect of wind. Export estimates were corrected for such variation in the present study. Lunar effects on tidal amplitude were corrected for by use of tide table information when calculating volume exchange on each day of the month. Wind effects were estimated by comparing amounts of material caught in fixed nets to that collected in freely swinging nets. Clumping of drifting plant material resulted in large variability in the amount of plant material collected between different nets. This is related in part to current and wind patterns which produced windrows of drifting material. Use of more and/or larger nets would help to reduce this type of variation in data in future studies.

Estimates of export made in the present study were compared to those reported recently in the Virgin Islands (Table 8). Rates for open beds in the 2 studies were similar, with values ranging from 0.23 to 0.56 g afdw m⁻² d⁻¹ for *Zostera marina* and *Halodule wrightii*, respectively at Harkers Island, and from 0.13 to 0.25 g afdw m⁻² d⁻¹ for *Syringodium filiforme* in the Virgin Islands (Zieman et al. 1979, Thayer et al. 1984). Leaf removal by grazing parrotfish was hypothesized to be a major factor in producing export of *S. filiforme* in the Virgin Islands. In Beaufort, the major factor affecting export is probably temperature-related stress during low tide and the interaction of winds and currents. At present, we cannot explain why the rates of blade export from these seagrass beds in the Virgin Islands and Beaufort were so similar. Nevertheless, large amounts of plant material were exported.

Table 8. Comparison of export of seagrass detritus by different species from different geographical areas

Species	Location	Export (g afdw m ⁻² d ⁻¹)	% of total monthly production exported	% of biomass	Source
<i>Zostera marina</i>	Phillips Island	0.01–0.26 ^a	6–8 ^b	1–20	This study
<i>Zostera marina</i>	Middle Marsh	0.05 ^b	0.9–2.5 ^b	0.9–2.5 ^b	This study
<i>Zostera marina</i>	Harkers Island	0.23–0.57 ^b	10–30 ^b	10–30 ^b	This study
<i>Halodule wrightii</i>	Middle Marsh	0.04 ^b	–	2–17	This study
<i>Halodule wrightii</i>	Harkers Island	0.23 ^b	–	40–75	This study
<i>Syringodium filiforme</i>	Tague Bay, Virgin Islands	0.13–0.25 ^c	60–100	–	Zieman et al. (1979)
<i>Thalassia testudinum</i>	Tague Bay, Virgin Islands	0.0 ^d	1	–	Zieman et al. (1979)

^a Annual range
^b Maximum summer value
^c Values given in afdw based on assumed 70 % organic content of *S. filiforme* (Zieman et al. 1982)
^d Based on assumed 70 % organic content (Zieman et al. 1979)

Export rates estimated in the present study can be compared to amounts of detritus entering the system from *Spartina alterniflora*, another major primary producer in this system. Williams (1973) estimated that the annual production of *S. alterniflora* in the study area amounted to 7.72×10^6 kg C yr⁻¹ (7720 t C yr⁻¹). Hopkinson & Hoffman (1984) estimated that from 10 to 50 % of the total amount of *S. alterniflora* produced in a Georgia estuary was exported. Assuming that this percentage is roughly the same for North Carolina marshes, the total amount of *S. alterniflora* exported from the North River estuary would range from 772 to 3860 t C yr⁻¹. Because this estimate includes DOC, it is not directly comparable to the 148 to 1573 t C yr⁻¹ of detritus estimated to be exported by *Zostera marina* in 1978, and 312 to 9674 t C yr⁻¹ estimated to be exported for 1976 and 1977 from Phillips Island. These estimates are based on a 38 % carbon content of live *Z. marina* (Thayer et al. 1977). An additional 600 t C yr⁻¹ has been estimated to be added as DOC as the result of excretion by eelgrass and its epiphytes (Penhale & Smith 1977). Export of *Z. marina* therefore equalled or exceeded that by *S. alterniflora* in this system.

Export of plant detritus from eelgrass beds in all likelihood plays a major role in the carbon cycle of the estuary near Beaufort. The large quantities and variety of types of materials produced indicate that export may contribute to a series of detrital pools of varying nutritional values. This may help promote secondary productivity throughout the year by maintaining a more constant food supply for detritivores. Although rates of export from seagrass beds vary greatly, the detritus itself probably plays an important ecological role in unvegetated portions of this estuary.

Acknowledgements. This material is based on research supported by the National Science Foundation under Grant No. OC77-07101. The senior author would also like to gratefully acknowledge the assistance given by Dr. T. R. Rice, Director of Southeast Fisheries Center's Beaufort Laboratory, for his generous cooperation in the completion of the project and for providing facilities. Sincere thanks are also extended to P. L. Bach for typing the draft manuscript, and to J. Kenworthy, M. Fonseca, and M. Robertson for their important contribution of ideas concerning the project.

LITERATURE CITED

- Blegvad, H. (1914). Food and condition of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. Rep. Dan. Biol. Stn 22: 41-78
- Dillon, C. R. (1971). A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph. D. thesis, Univ. North Carolina, Chapel Hill
- Gallagher, J. L., Kibby, H. V., Skirvin, K. W. (1984). Detritus processing and mineral cycling in seagrass (*Zostera*) litter in an Oregon salt marsh. Aquat. Bot. 20: 97-108
- Harrison, P. G., Mann, K. H. (1975). Detritus formation from eelgrass (*Zostera marina*) L.: the relative effects of fragmentation and decay. Limnol. Oceanogr. 20: 924-934
- Hopkinson, C. S., Hoffman, F. A. (1984). The estuary extended - a recipient system study of estuarine outwelling in Georgia. In: Kennedy, V. S. (ed.) The estuary as a filter. Academic Press, New York, p. 313-330
- Josselyn, M. N. (1978). The contribution of marine macrophytes to the detrital pool of the Great Bay estuary system, N. H. Ph. D. thesis, Univ. New Hampshire, Durham
- Josselyn, M. N., Mathieson, A. C. (1980). Seasonal influx and decomposition of autochthonous macrophyte litter in a north temperate estuary. Hydrobiologia 71: 197-208
- Kenworthy, W. J. (1981). The interrelationship between seagrasses, *Zostera marina* and *Halodule wrightii*, and the physical and chemical properties of sediments in a mid-Atlantic coastal plain estuary near Beaufort, North Carolina (USA). M. S. thesis, Univ. Virginia, Charlottesville
- Kenworthy, W. J., Thayer, G. W. (1984). Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum* in temperate and subtropical marine ecosystems. Bull. mar. Sci. 35 (3): 364-379
- Marshall, N. (1970). Food transfer through the lower trophic levels in the marine environment. In: Steele, J. H. (ed.), Marine food chains. Univ. California Press, Berkeley, pp. 52-56
- McRoy, C. P., Helfferich, C. (ed.) (1977). Seagrass ecosystems: a scientific perspective. M. Dekker, New York
- Menzies, R. J., Rowe, G. T. (1969). The distribution and significance of turtle grass *Thalassia testudinum* on the deep sea floor off North Carolina.
- Menzies, R. J., Zaneveld, J. S., Pratt, R. M. (1967). Transported turtle grass as a source of organic enrichment of abyssal sediments off North Carolina. Deep Sea Res. 14: 111-112
- Nixon, S. W. (1980). Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In: Hamilton, P., MacDonald, K. B. (ed.) Estuarine and wetland processes. Plenum Publ. Corp., New York, p. 437-525
- Ostenfeld, C. H. (1908). On the ecology and distribution of grass wrack (*Zostera marina*) in Danish waters. Rep. Dan. Biol. Stn 16: 1-62
- Penhale, P. A. (1977). Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. J. exp. mar. Biol. Ecol. 26: 211-224
- Penhale, P. A., Smith, W. O., jr. (1977). Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) community. J. exp. mar. Biol. Ecol. 26: 211-224
- Petersen, C. G. J. (1918). The sea bottom and its production of fish food. A survey of the work done in connection with valuation of the Danish waters from 1883-1917. Rep. Dan. Biol. Stn 25: 1-82
- Petersen, C. F. J., Boysen-Jensen, P. (1911). Valuation of the sea. I. Animal life of the sea bottom, its food and quantity. Rep. Dan. Biol. Stn 20: 1-81
- Tenore, K. R. (1977). Growth of the polychaete, *Capitella capitata*, cultured on different levels of detritus derived from various sources. Limnol. Oceanogr. 22: 936-941
- Thayer, G. W., Wolfe, D. A., Williams, R. B. (1975a). The impact of man on seagrass systems. Am. Scient. 63: 288-296
- Thayer, G. W., Adams, S. M., LaCroix, M. W. (1975b). Structural and functional aspects of a recently established *Zostera marina* community. In: Cronin, L. E. (ed.) Estuarine research. Vol. 1. Academic Press, New York, p. 518-540

- Thayer, G. W., Engel, D. W., LaCroix, M. W. (1977). Seasonal distribution and changes in the nutritive quality of living, dead and detrital fractions of *Zostera marina* L. J. exp. mar. Biol., Ecol. 30: 109-127
- Thayer, G. W., Kenworthy, W. J., Fonseca, M. S. (1984). Ecology of eelgrass meadows of the Atlantic Coast: A community profile. U. S. Fish and Wildl. Serv. Publ. no. FWS/OBS-84/02
- Williams, R. B. (1973). Nutrient levels and phytoplankton productivity in the estuary. In: Chabrek, R. H. (ed.) Proceedings of the coastal marsh and estuary management symposium. Louisiana State University, Baton Rouge, p. 58-89
- Wolff, T. (1976). Utilization of seagrass in the deep sea. Aquat. Bot. 2: 161-174
- Zieman, J. E. (1975). Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. In: Cronin, L. E. (ed.) Estuarine research. Vol. 2. Academic Press, New York, p. 541-562
- Zieman, J. C., Thayer, G. W., Robblee, M. B., Zieman, R. T. (1979). Production and export of seagrasses from a tropical bay. In: Proceedings of conference on biological processes in coastal and marsh systems. Plenum Press, New York, p. 21-33
- Zieman, J. C. (1982). The ecology of the seagrasses of South Florida: a community profile. U. S. Fish and Wildl. Serv. Publ. no. FWS/OBS-82/25

This paper was submitted to the editor; it was accepted for printing on October 11, 1985