Oxygen production and consumption associated with the major autotrophic components in two temperate seagrass communities*

Laura Murray** & Richard L. Wetzel

College of William and Mary, School of Marine Science and Virginia Institute of Marine Science,
Gloucester Point, Virginia 23062, USA

ABSTRACT: Oxygen production and comsumption rates were determined for the various communities (plankton, sediment, and seagrass-plus-epiphytes) associated with 2 adjacent seagrass communities, one dominated by *Zostera marina* and the other by *Ruppia maritima*. Annual estimates of gross production summed for all communities were high compared to other reports (ca 1600 gC m^{-2} and 1100 gC m^{-2} in the *Z. marina* and the *R. maritima* dominated communities, respectively). Plankton and sediment communities accounted for ca 45 and 36 % in the 2 areas, respectively. Seasonal patterns of production for the 2 areas differed. In the *Z. marina* area, plankton and sediment production dominated during summer, whereas in the *R. maritima* area production of seagrass (plus epiphytes) dominated throughout the study. Temporal trends for oxygen production and consumption of the plankton and sediment components corresponded closely and suggested direct *in situ* utilization. However, a lag observed between production and consumption in the seagrass-plus-epiphyte component indicated indirect utilization mediated by microbially dominated decomposition and remineralization processes. The ratio of annual gross production to dark respiration (P:R) exceeded 1.0 in both seagrass communities and for all components, suggesting net export and/or burial of carbon in these systems.

INTRODUCTION

Seagrass communities are characterized by diverse autotrophic and heterotrophic populations including many commercially important macrofaunal species. In addition to the vascular plants, several other components contribute to community production, including benthic microflora. This diversity in primary producers theoretically provides numerous pathways for the secondary utilization of organic matter (Thayer et al. 1975) and contributes to a greater abundance and diversity of heterotrophic organisms in seagrass beds relative to unvegetated sediment habitats (Orth 1973, Stoner 1980). Whereas direct grazing on living seagrasses tends to be limited (Thayer et al. 1975), microalgal populations (planktonic, sediment and epiphytic) provide a direct energy/organic matter source for higher trophic level consumers that may equal or even exceed the trophic importance of the vascular plant (Zimmerman et al. 1979, Morgan 1980). Seagrass systems are utilized heterotrophically by a large number of epifaunal, infaunal, benthic, and pelagic macrofauna, including many commercially important species such as the blue crab (Heck & Orth 1980). Microbial processes account for vascular plant decomposition, which provides food for yet another group of heterotrophic species.

Most previous studies on primary production in seagrass communities either have focused on the dominant vascular plant species (McRoy 1974, Zieman & Wetzel 1980) or report estimates of total production for the entire community (Nixon & Oviatt 1972, Neinhuis 1980, Lindeboom & deBree 1982, Wetzel 1983). The ecological significance of the various microalgal components has received limited attention and remains poorly documented. Considerable research in freshwater (Wetzel 1964, Sondergaard & Sand-Jensen 1978, Cattaneo & Kalff 1980) and a few studies in marine environments (Marshall et al. 1971, Thayer et al. 1975)
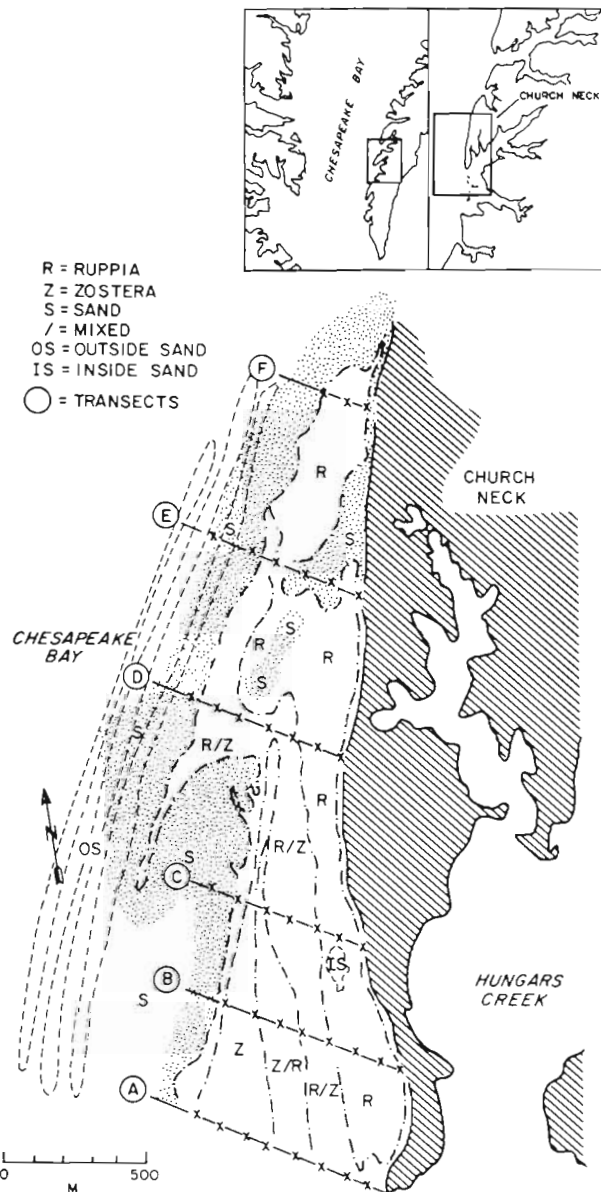

Fig. 1. Location of study site and plant community distribution at Vaucluse Shores, Chesapeake Bay, Virginia, USA

(1982) found that both production and consumption were significantly greater in *Zostera marina* L. beds than in nearby unvegetated areas, indicating higher, heterotrophic metabolic activity within the grass beds. However, specific rates of production and respiration for macrophytes, epiphytes, plankton and sediment have not been quantified previously for a seagrass community.

The purpose of this study was to compare the relative contributions of several operationally defined autotrophic groups to community production in 2 adjacent seagrass communities, the principal components being seagrass-plus-epiphyte, sediment, and plankton. For this study the vascular plant and epiphyte components are combined due to the low abundance of epiphytes (Murray 1983). Concurrently, we examined oxygen respiration for the biota associated with each of these groups. Previous studies had demonstrated that seasonal patterns of vascular plant abundance were distinctly different for the 2 communities investigated, one dominated by *Zostera marine* L. and the other by *Ruppia maritima* L. (Wetzel & Penhale 1983). We hypothesized that seagrass systems with distinctly different patterns of abundance would also have varying patterns of microalgal production, with rates increasing during periods of declining macrophyte production. Patterns of organic matter utilization within the system (as reflected by oxygen consumption rates) would be expected to closely follow production where direct utilization was the dominant heterotrophic mode, while production and consumption for detrital-based or indirect pathways would be out of phase.

MATERIALS AND METHODS

Study site. The investigations reported here were conducted in a seagrass meadow approximately 140 ha in size located on the southeastern shore of Chesapeake Bay, Virginia, USA (37° 25′N, 75° 59′W), in an area known locally as Vaucluse Shores (Fig. 1). Nearshore areas were dominated by *Ruppia maritima*, while *Zostera marina* was the dominant vascular plant occupying the deeper areas. An intermediate area was comprised of mixed stands of the 2 species. The area is partially protected from heavy wave action by an offshore sand-bar. Mean water depths in the *Z. marina* and *R. maritima* communities were approximately 1.0 and 0.5 m, respectively (tidal range of 0.5 m). Sediments in the study area were generally sandy and relatively low in organic content (Wetzel 1983). Ranges in salinity and temperatures were 17 to 25 ‰ and 0 to 30 °C for both sites during this study. A more detailed description of the area has been given by Wetzel & Penhale (1983).

have shown that the contribution of microalgal can account for 30 to 60 % of total annual community production. At certain times production by epiphytic microalgae can equal that of host seagrasses (Penhale 1977, Borum & Wium-Andersen 1980, Morgan & Kitting 1984).

Although several studies have examined primary production of epiphytic and planktonic algae in seagrass communities, few have coupled these with rates of consumption (Morgan & Kitting 1984). Hargrave (1969) reported a higher benthic carbon consumption rate than could be supported by vascular plant production alone in a freshwater lake. Lindeboom & deBree

Oxygen production and consumption: general procedures. Oxygen production and consumption associated with the operationally defined autotrophic groups in the 2 seagrass communities were estimated from the rate of change in dissolved oxygen concentration during incubations using various enclosure designs described below. Dissolved oxygen concentrations were measured using a multichannel system of Clark-type polargraphic electrodes with built-in stirrers (Orbisphere Model #2604), calibrated against water-saturated air for each experiment. Light as photosynthetically active radiation (PAR: 400 to 700 nm) was monitored continuously using surface and submarine cosine-corrected quantum sensors (LiCor Model 185A) placed 20 cm above the sediment surface within the seagrass canopy. Temperature was recorded continuously during each incubation from sensors contained in the O_2 electrodes. All experiments were conducted during mid-day hours (1000 to 1400 h). Daily O_2 production and consumption (e.g. dark respiration) rates were calculated assuming the mean rates over the incubation interval to be representative of the entire photoperiod (defined as 80 % of daylight hours; Wetzel 1983). Estimates of seasonal O_2 production and consumption were derived by defining seasons according to ambient water temperature. For the *Zostera marina* community seasons were defined as: winter, $< 10\,°C$; spring and fall, 10 to $20\,°C$; summer, $> 20°C$. For the *Ruppia maritima* community spring and fall were defined by water temperatures between 10 and $25\,°C$, while summer was defined as temperatures $> 25\,°C$. Linear interpolations were used between consecutive monthly measurements and integrated over the year to estimate annual rates. Wetzel & Penhale (1983) provide a detailed explanation for these seasonal definitions in relation to temperature. Because all experiments were purposefully conducted at or near optimum *in situ* light conditions, the extrapolated seasonal and annual gross and net productivity estimates are maximum potential rates and do not reflect the inherent day-to-day climatic variability characteristic of these systems that would make realized rates lower (Wetzel 1983, Wetzel & Penhale 1983, Wetzel & Neckles 1986). For comparison with values reported elsewhere, the oxygen data were converted to carbon equivalents by assuming a photosynthetic quotient (PQ) of 1.25 and a respiratory quotient (RQ) of 1.0 (Lindeboom & deBree 1982, Oviatt et al. 1986).

Plankton O_2 production and consumption. Plankton samples were collected using a Van Dorn water sampler from 10 cm below the water surface and from just above the canopy top in the *Zostera marina* area. Triplicate light and dark bottle incubations were conducted in standard BOD bottles (300 ml) which were suspended at the depth of collection. For the shallower

Ruppia maritima community samples were collected from and incubated at mid-depth only (ca 25 cm below the water surface). Oxygen concentrations in the BOD bottles were determined 3 times during each incubation (beginning, middle and end). Areal rates of O_2 production and consumption were estimated using the average water depth over the incubation interval.

Sediment O_2 production and consumption. Production and consumption of O_2 by the sediment community (including microautotrophic and heterotrophic organisms) were estimated using triplicate clear and opaque acrylic chambers covering a sediment surface area of 60 cm and containing 750 ml of ambient water. Concentrations of O_2 were measured 3 times over the incubation interval using a polargraphic electrode (with stirrer) inserted through a port in the top of the chambers. The chambers were placed among the vascular plants but in sediments without seagrass leaves. Sediment O_2 production and consumption estimates were corrected for the water (plankton) contribution to O_2 changes during incubation. Areal estimates were derived by estimating the bare sediment surface area within the vascular plant communities using percent cover and plant abundance data reported by Orth et al. (1979) and Wetzel (1983).

Seagrass-plus-epiphyte O_2 production and consumption. In these seagrass communities the abundance of an attached, epiphytic community was relatively low, representing $< 7 \%$ of the combined dry mass of seagrass leaves and epiphytes (Murray 1983). Therefore, rate estimates for epiphytes and the seagrass hosts (seagrass-plus-epiphyte) were combined for the purposes of this study. Rates of O_2 production and consumption were calculated as the difference between estimates for the total community and the combined rates of the sediment and plankton. Total community production and consumption were measured as oxygen exchanges under large (260 l; 0.78 m surface area) plexiglass dome enclosures and are described in detail elsewhere (Wetzel 1983, Wetzel & Penhale 1983).

RESULTS

Measurements of O_2 production and consumption in *Zostera marina* and *Ruppia maritima* communities were conducted during various conditions, with water temperature ranging from 7 to 29 °C. For these studies, light (PAR) conditions at 20 cm above the sediment within the seagrass canopy were generally at or above photosynthetic saturation intensities for both vascular plants (ca 200 to 400 $\mu E\ m^{-2}\ s^{-1}$; Wetzel & Penhale 1983) and microalgae (ca 30 to 100 $\mu E\ m^{-2}\ s^{-1}$; Cadee & Hegeman 1974, Admiraal 1977). However, for *Z. marina* during April, early October and January studies

and for *R. maritima* during the October study PAR levels were below saturation. Experimental conditions for all studies are summarized in Table 1.

Net apparent productivity (NAP; O_2 evolution during daylight hours) and respiration (as oxygen consumption) estimates for *Zostera marina* communities were dominated by the seagrass-plus-epiphyte component during winter, spring and late fall, while during mid-summer plankton contributions were of greater importance (Fig. 2). This shift in relative productivity corresponds with a mid to late summer die-back of *Z. marina*, which is characteristic for these seagrass populations in lower Chesapeak Bay (Wetzel 1983, Wetzel & Penhale

1983). Respiration of the seagrass-plus-epiphyte component increased as NAP decreased following a May peak in productivity, indicating a lag between production and respiration. In contrast, the plankton and sediment components exhibited close temporal correspondence of NAP and respiration throughout the year.

Net apparent productivity and respiration (Fig. 3) for *Ruppia maritima* exhibited summer peaks in activity, which is consistent with maximum biomass for *R. maritima* during mid to late summer (Orth et al. 1979, Wetzel 1983). Compared to the *Zostera marina* community, the *R. maritima* seagrass-plus-epiphyte complex clearly dominated throughout the study period.

Table 1. Experimental conditions during O_2 production and respiration studies at 2 seagrass sites. Data given are arithmetic means over incubation period

Month & Date	Seagrass system	Temperature (°C)	PAR ($\mu E\ m^{-2}\ s^{-1}$)[*]		Seagrass abundance[**]	
			Surface	Bottom	Biomass (g dwt m^{-2})	Cover (%)
March						
10 Mar 81	Zostera	8	nd	266	nd	nd
April						
9 Apr 81	Zostera	14	396	104	nd	nd
May						
8 May 81	Zostera	16	1860	275	96	93
22 May 81	Zostera	18	1664	395	81	85
June						
15 Jun 81	Zostera	26	1593	323	116	100
14 Jun 81	Ruppia	24	nd	627	20	nd
30 Jun 81	Ruppia	25	nd	nd	34	nd
July						
13 Jul 81	Zostera	33	1183	266	62	70
15 Jul 81	Ruppia	24	nd	720	80	nd
August						
4 Aug 81	Zostera	27	1645	294	61	69
25 Aug 81	Zostera	26	1650	285	19	28
4 Aug 81	Ruppia	27	nd	355	82	nd
26 Aug 81	Ruppia	25	nd	469	87	nd
September						
15 Sep 81	Ruppia	27	nd	371	61	nd
October						
13 Oct 81	Zostera	20	1204	125	24	33
22 Oct 81	Zostera	16	1191	222	nd	nd
13 Oct 81	Ruppia	20	nd	125	70	nd
January						
6 Jan 82	Zostera	7	384	132	nd	nd

[*] PAR is photosynthetically active radiation (400 to 700 nm); surface refers to measurements in air; bottom indicates in water, 20 cm from sediment surface
[**] Biomass data from Wetzel (1983); percent cover estimated using these biomass data and a biomass-% cover regression (r = 0.95) developed from data of Orth et al. (1979)
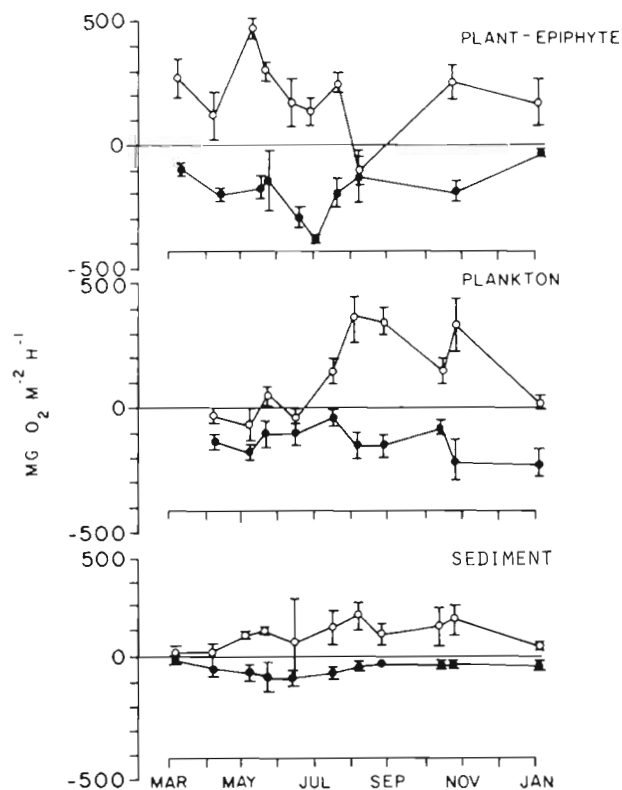nd: not determined

Fig. 2. *Zostera marina* dominated community. Mean (± SD) areal estimates of net apparent productivity (○) and respiration (●) for the 3 autotrophic components

The July peak in seagrass-plus-epiphyte NAP coincided with the decline in NAP of the same component in the *Z. marina* community. Respiration for *R. maritima* (plus epiphytes) tracked NAP during the initial growth period but increased during plant die-back in the fall. Plankton and sediment metabolic rates were considerably lower and only comprised a maximum of 30 % of the total community NAP or respiration. Both components exhibited higher productivity rates during early summer (June to August), but declined in late summer and fall. Plankton respiration rates followed NAP rates. However, sediment respiration exhibited an increase in rate (August) corresponding to the decline in plant NAP.

Seasonal and annual estimates of gross production (defined as the algebraic sum of NAP and respiration) for the *Zostera marina* community and its epiphytes accounted for between 37 and 80 % of total gross production depending on season, with annual rates of ca 867 gC m^{-2} yr^{-1} (Table 2). Plankton and sediment gross production ranged from 10 to 48 % and 10 to 25 % of the total with annual rates of ca 488 and 225 gC m^{-2} yr^{-1}, respectively. Respiration of the seagrass and epiphytes dominated the total for all seasons except winter, accounting for 42 % of total annual O_2 consumption. Respiration rates for plankton and sediment
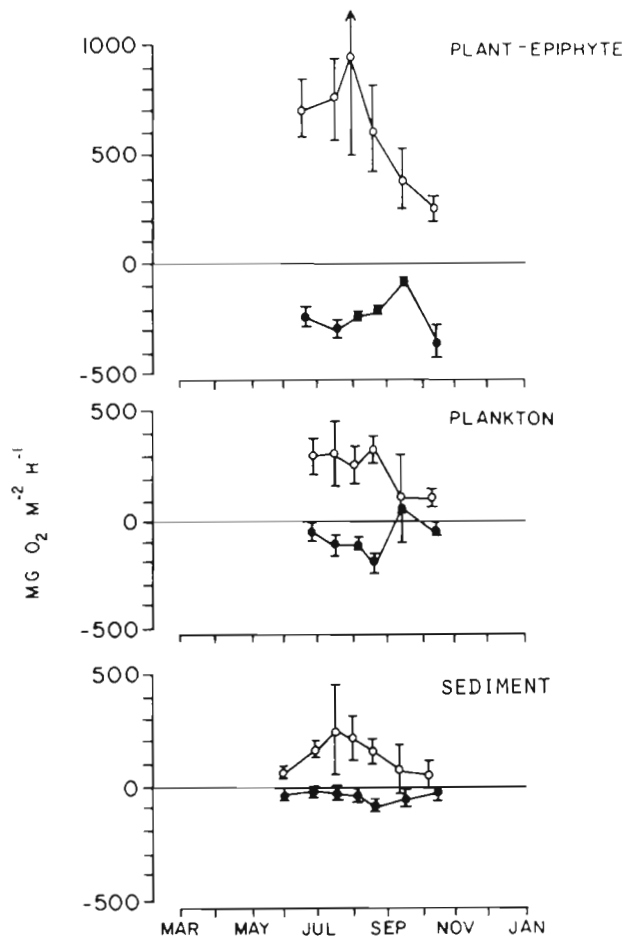

Fig. 3. *Ruppia maritima* dominated community. Mean (± SD) areal estimates of net apparent productivity (○) and respiration (●) for the 3 autotrophic components

communities were relatively important in winter and summer seasons, respectively.

In the *Ruppia maritima* community (Table 3) gross production by seagrass-plus-epiphytes constituted a greater proportion of the total, ranging from 44 to 76 %, with an annual contribution of 707 gC m^{-2} yr^{-1}. This estimate of annual production assumes that winter productivity of *R. maritima* is negligible, an assumption consistent with observations of denudation associated with ice sheeting and natural mortality (Murray 1983). The combined annual contributions of all microalgae components was considerably less important in this community compared to the *Zostera marina* system (36 vs 45 % of the total). The partitioning of total respiration in the *R. maritima* community was similar to that for gross production.

The ratio of daily production to respiration (P:R) indicates the balance between autochthonous production and consumption of organic matter for each component in the 2 communities (Tables 2 & 3). Overall, P:R ratios for total community metabolism were gener-

Table 2. Seasonal and annual estimates of gross production (P) and respiration (R) (gC m^{-2}) by the principal components and total community in the *Zostera marina* area (n = 11)

Component	Winter P	Winter R	Spring P	Spring R	Summer P	Summer R	Fall P	Fall R	Annual total* P	Annual total* R	Annual total* Net
Seagrass-plus-epiphytes	330	53	289	105	161	140	87	117	867	415	452
% of total	55	18	80	51	41	47	37	60	55	42	76
Component P:R	6.2		2.8		1.2		0.74		2.1		
Plankton	205	213	36	72	134	87	113	62	488	434	54
% of total	34	73	10	35	34	30	48	32	31	44	9
Component P:R	0.96		0.50		1.5		1.8		1.1		
Sediment	63	25	32	30	95	68	35	15	225	138	87
% of total	11	9	10	14	25	23	15	8	14	14	15
Component P:R	2.5		1.1		1.4		2.3		1.6		
Total	598	291	357	207	390	295	235	194	1580	987	593
P:R	2.0		1.7		1.3		1.2		1.6		

* Rates are maximized due to calculation method (i.e. midday rates extrapolated to the photoperiod, and constant respiration for the diel period)

ally > 1.0 for both communities, the notable exceptions being the seasonal die-back periods for both vascular plant species. In terms of organic matter input to the communities (i.e. excess production versus respiration), the relatively high production rates combined with high P:R ratios for seagrass-plus-epiphyte components in both systems indicated their dominant importance. Although P:R ratios were high for the sediment communities (especially in the shallower *Ruppia maritima* system), their overall inputs to the respective community budgets for organic matter are relatively low. A lag between production and consumption for the seagrass-plus-epiphyte component is evident in that peak pro-

duction occurs in the spring for both communities, while peak consumption occurs in summer and fall for *Zostera marina* and *R. maritima* communities, respectively.

Pair-wise linear regressions between metabolic rates and selected environmental parameters (temperature and light), as well as vascular plant biomass revealed that respiration was significantly correlated with temperature for all components in the *Zostera marina* community, as might be expected. In this system, net productivity was positively correlated with temperature for the sediment (r = 0.65; n = 11) suggesting microalgal response to temperature increases. No significant cor-

Table 3. Seasonal and annual estimates of gross production (P) and respiration (R) (gC m^{-2}) by the principal components and total community in the *Ruppia maritima* area (n = 16)

Component	Spring P	Spring R	Summer P	Summer R	Fall P	Fall R	Annual total* P	Annual total* R	Annual total* Net
Seagrass-plus-epiphyte	306	192	259	128	142	172	707	492	215
% of total	76	76	69	80	44	46	64	62	69
Component P:R	1.6		2.0		0.8		1.4		
Plankton	66	54	71	27	150	190	287	291	16
% of total	16	22	19	17	46	50	26	34	5
Component P:R	1.2		2.6		0.8		1.1		
Sediment	30	5	45	6	31	15	106	26	80
% of total	8	2	12	3	10	4	10	4	26
Component P:R	6.0		7.5		2.1		4.1		
Total	402	251	375	161	323	377	1100	789	311
P:R	1.6		2.3		0.8		1.4		

* Assuming 0 in winter. Rates are maximized due to calculation method (i.e. midday rates extrapolated to the photoperiod, and constant respiration for the diel period)

relation could be found between PAR and NAP for any component in the *Z. marina* community, indicating that light was not limiting. This result is as expected due to the experimental design; i.e. incubations were conducted during optimal light conditions. Biomass of *Z. marina* was positively correlated with seagrass-epiphyte respiration, but negatively correlated with benthic respiration ($r = -0.76$; $n = 11$). These correlations may suggest plant senescence after peaks plant-growth periods, and shading of sediment microalgae by the seagrass. NAP of both the *Ruppia maritima* seagrass-plus-epiphyte and the sediment community were positively correlated with temperature (see above) ($r = 0.62, 0.61, P < 0.10; n = 6$); however, respiration was not significantly correlated with temperature for any of the components perhaps due to experimental design (i.e. no winter measurements). Productivities of both *R. maritima* and associated sediment community were weakly correlated with light ($r = 0.61, 0.62, P < 0.10; n = 6$), again as expected due to experimental design. Plankton productivity in the shallow *R. maritima* area, however, was negatively correlated with light ($r = -0.70, P < 0.10; n = 6$), perhaps due to photoinhibition (Fisher et al. 1982).

DISCUSSION

Annual rates of net production of seagrasses (plus epiphytes) in this study were ca 300 and 500 gC m^{-2} for *Ruppia maritima* and *Zostera marina*, respectively, which corresponds well with measurements reported for these species using a variety of techniques (Dillon 1971, McRoy 1974, Verhoeven 1979, Neinhuis 1980, Thorne-Miller & Harlin 1984). In the *Z. marina* community annual mean epiphyte biomass was < 10 % of the total combined seagrass-plus-epiphyte (above ground) dry weight, and epiphyte production (NAP) was < 7 % of the combined rate for the community (Murray 1983). These epiphytic biomass and production rates are low compared to other temperate seagrass systems which typically range from 25 to 60 % (Penhale 1977, Borum & Wium-Andersen 1980, Morgan & Kitting 1984). Seagrasses (and their epiphytes) here contributed 55 and 64 % of the total annual carbon produced in the *Z. marina* and the *R. maritima* communities, respectively. The remaining autochthonous production was provided by the associated sediment and planktonic communities.

Net production estimates for individual microalgal (plankton & sediment) components in these seagrass communities were similar to those of other studies. Annual production for the sediment community in the *Zostera marina* and the *Ruppia maritima* communities were 225 and 106 gC m^{-2}, respectively. These values

are in the range of previous reports for production in a variety of sediment types (Pomeroy 1959, Grontved 1960, Pamatmat 1968, Marshall et al. 1971, Riznyk & Phinney 1972, Joint 1978, Zelder 1980, Rizzo & Wetzel 1985, Rizzo 1986). The contributions of the sediment to total annual production in these seagrass systems were 3 and 14 % which brackets the 8 % reported by Thayer et al. (1975) for a *Z. marina* community in North Carolina. Net annual plankton production estimates for the *Z. marina* and *R. maritima* areas in this study were 488 and 287 gC m^{-2}, respectively. Increased *in situ* light conditions and close coupling of sediment-water column remineralization may account for these relatively high rates of plankton production.

Although overall production values for the 2 communities are similar, the seasonal patterns and relative contributions of individual components were quite different. In the *Zostera marina* area a summer decline in seagrass production was observed. However, net community production remained high because increased microalgal production during this period compensated for decreased seagrass production. On the other hand, seagrass-plus-epiphyte production in the *Ruppia maritima* community was positively correlated with temperature, and peak production occurred in mid-summer followed by a decline in fall. Here, microalgae followed a seasonal pattern similar to that of the seagrass. Thus, the decline in seagrass production was not accompanied by an increase in production of the plankton and sediment communities.

Respiration values provide a further indication of differences between the 2 communities in relation to heterotrophic utilization of primary production. The combined respiration of plankton and sediment accounted for 58 % of total respiration in the *Zostera marina* area, compared to 38 % in the *Ruppia maritima* system, indicating a greater importance of water-column and sediment food chains in the former. Relatively high respiration rates for the seagrass-plus-epiphyte component of both communities during summer may reflect increases in both respiration (Bieble & McRoy 1971) and excretion of dissolved organic carbon (and associated bacterial respiration; Kirchman et al. 1984) resulting from elevated temperatures. The increased respiration and decreased P:R ratios of the seagrass (plus epiphytes) in both communities and especially *R. maritima* probably indicate plant senescence and heterotrophic decomposition of seagrass stands (Godshalk & Wetzel 1978). In both areas, the seagrass-plus-epiphyte component exhibited a lag between production and respiration, suggesting perhaps that heterotrophic utilization of seagrass production is *indirect* (i.e. utilized via detrital pathways). Further support for this concept is evident in the seasonal sequence of P:R ratios for the seagrass-plus-epiphyte complex. In both

the *Z. marina* and *R. maritima* areas, P:R declined following peaks in NAP (i.e. late summer and fall, respectively). This trend is consistent with the concept that seagrass production is utilized predominantly through decomposition processes (Hargrave 1969, Lindeboom & deBree 1982, Wetzel 1983). In contrast, the microalgal components exhibited a strong temporal correspondence between NAP and respiration, suggesting more direct pathways for utilization of production. However, benthic respiration in the *R. maritima* area was more closely coupled with the onset of seagrass die-back, with peak rates in August.

We have demonstrated here that autotrophic communities associated with 2 temperate seagrasses are characterized by high rates of oxygen (and presumably organic matter) production, and that the seagrasses plus epiphytes themselves contribute only 55 to 64 % of the total gross production. Most previous studies have ignored one or more of the microalgal components of these communities, thereby, at least potentially, underestimating total primary production. The 2 seagrass communities studied here exhibited distinctly different temporal patterns of production, one of which *(Zostera marina)* was asynchronous with that of the sediment plus planktonic algae and the other of which *(Ruppia maritima)* corresponded closely to the temporal sequence of microalgal production. Indirect evidence suggests that microalgal production is utilized more directly than that of seagrasses, and annual carbon budgets estimated for those 2 systems indicate that there is excess autochthonous (the value would be even greater if equivalent PQ and RQ values were used) production (above consumption) which is either buried in place or exported to contiguous estuarine habitats.

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