Temporal biomass variability and production/ biomass relationships of seagrass communities

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ABSTRACT· Data on biomass variability and production/biomass ratios of seagrass communities were analysed to describe the relationship between the trophic (i.e. primary production) and structural (i.e. biomass) roles of marine submerged macrophytes. The analyses revealed that most (>70%) of the biomass variability appears to reflect seasonal responses, and that the extent of variability is constrained by the latitudinal position of the plant stands, those at lower latitudes sustaining a more uniform biomass throughout the year. Annual production/biomass ratios are quite variable, although tend to be greater (average = 4.6) than those for freshwater submerged plants, and tend to increase at lower latitudes. This trend is not attributable to greater daily production/biomass ratios for tropical and subtropical communities, but appears to be a consequence of their small biomass seasonality.

INTRODUCTION

Seagrass communities play 2 primary roles in coastal marine ecosystems: (1) a trophic role, through their direct contribution to ecosystem primary production (e.g. Zieman 1982, Thayer et al. 1984, Murray & Wetzel 1987), and (2) a structural role (Kenworthy et al. 1988), because seagrass stands provide surfaces for epiphytic growth (Penhale 1977, Borum & Wium-Andersen 1980) and shelter to animal communities (e.g. Heck & Orth 1980, Kenworthy et al. 1988), thereby sustaining a diverse food-web (see reviews by Zieman 1982, Thayer et al. 1984, Kenworthy et al. 1988). These 2 roles are strongly coupled because the often small direct consumption of seagrass tissues (e.g. Thayer et al. 1975) results in the accumulation of primary production as seagrass biomass, which presumably determines seagrass structural importance.

The link between the trophic and the structural roles of seagrass communities can best be investigated by quantifying the relationship between biomass and primary production. Because macrophyte biomass is a cumulative property, the relationship between the biomass and annual production of seagrass communities (P/B ratio) has often been established on the basis of the maximum biomass attained by the community (e.g. Thorne-Miller & Harlin 1984, Kentula & McIntire 1986).

The structural importance of seagrass communities, however, is only partially represented by their maximum biomass because this reflects their maximum importance, but not the temporal variability of their structural influence (i.e. biomass variability). Quantification of biomass variability is important to any evaluation of the role of seagrass communities because this variability influences whether the export of organic carbon – to the underlying sediments or out of the seagrass meadow – is a continuous (i.e. small variability) or abrupt (i.e. high variability) process (e.g. Frankignoulle & Bouquegnau 1987), and because biomass variability also determines the temporal variability in habitat structure experienced by seagrass-associated biota. Further, biomass variability may influence the associated biota differently depending on whether the changes are seasonal (predictable), or aseasonal (unpredictable).

Here I present a first analysis of the relationship between the structural and trophic roles of seagrass communities, and of the temporal distribution of their structural influence. Because of the postulated importance of latitude in the degree of biomass variability of seagrass communities (Orth & Moore 1986), I appraise the relationship between the different aspects of biomass variability and the latitudinal position of the plant communities. I then describe the relationship between the production and biomass of seagrass communities both on an annual and on a daily basis. To maximize the generality of the analyses I used available data on the biomass and production of a wide variety of marine angiosperm communities (Tables 1 and 2).

270

Mar Ecol. Prog. Ser 51: 269–276, 1989

METHODS

Biomass variability was characterized from the variability about the annual mean biomass of the seagrass community, quantified as the coefficient of variation, and from the time of the year (i.e. month) when peak biomass was measured. The coefficient of variation of the annual biomass, which allows direct comparisons among the relative variabilities of communities differing in absolute biomass, was obtained from the available literature comprising at least bimonthly estimates of plant biomass for the periods when significant macrophyte biomass occurred. The time of maximum biomass was estimated using only literature reporting at least monthly biomass values.

To assess whether the observed biomass variability reflected seasonal or aseasonal processes I fitted a second order polynomial to the annual biomass data

$$\text{Biomass} = a + b_1 \text{ Time} + b_2 \text{ Time}^2 \qquad (1)$$

where Time is the number of months past winter solstice. Significant fits to the second order polynomial (i.e. $p < 0.05$ for t-test on b_1 and b_2) indicate seasonality in plant biomass variation, whereas non-significant fits suggest aseasonal growth patterns.

The majority of the data on annual and daily macrophyte production rates were obtained with shoot or leaf marking techniques, but I also included estimates obtained with ^{14}C incorporation and O_2 evolution techniques. The comparison of results from different techniques should have little impact on the analysis because differences among techniques are minor compared to the broad ranges in plant production contained in the data set (Bittaker & Iverson 1976, Kemp et al. 1986). Nevertheless, I used analysis of covariance to test for any bias among the different techniques that could account for the patterns revealed in the analyses.

The annual balance between production and biomass was established by comparing annual production estimates with maximum aboveground biomass of the stand, and daily production-biomass balances were established by comparing daily production estimates with the aboveground biomass of the stand studied. Biomass and production estimates were transformed, when necessary, to dry weight assuming ash-free dry weight to be 80 % of dry weight, and organic carbon to be 37 % of dry weight (Westlake 1974). Variation around these conversion factors is expected to increase the error in the analysis, although this effect should be small because these conversions were used on less than 20 % of the annual data and less than 40 % of the daily data.

RESULTS

Data base

The data set included information pertaining to communities of 11 species of submerged angiosperms (Tables 1 and 2), all but 2 of them (i.e. *Ruppia* spp.) being marine seagrasses. A significant fraction of the literature on marine angiosperms refers to *Zostera marina*. The communities were located across a broad latitudinal range (9 to 59°), although most of the communities were temperate. Because few studies included sufficient data on biomass seasonality and annual production to be used in all analyses, the data sets used in each step of the analysis differ.

Biomass variability

The extent of annual biomass variability differed greatly among macrophyte communities (biomass coefficient of variation ranged from 17 to 120 %), from communities with small coefficients of variation to communities experiencing very dramatic variations.

Most of the communities showed biomass variability that fitted (t-test, $p < 0.05$ for b_1 and b_2 in Eq. 1) a seasonal model, although the variability in a tropical (9°S; Broums & Hejs 1986) and a subtropical (27° S; Boon 1986) seagrass community did not conform to the seasonal model. Seasonal changes accounted, on average, for ca 70 % of the biomass variability of the communities (average $r^2 = 0.67$, maximum 0.94). The extent of variability tended to be greater for macrophyte communities in higher latitudes (r for latitude-variability $= 0.43$; $p < 0.05$; Fig. 1). Closer examination of the relationship between biomass variability and latitude (Fig. 1) suggests the existence of a latitude-dependent upper boundary to biomass variability rather than a tight linear relation between the 2 variables.

Most of the communities achieved their maximum biomass between July and August (January for southern hemisphere communities, Fig. 2), irrespective of their latitudinal position ($r = -0.14$, $p > 0.05$).

Production/biomass relationships

Peak biomass and annual production of seagrass communities ranged over an order of magnitude (Table 3), although variability in annual production was somewhat smaller (coefficient of variation $= 52$ %) than that in peak biomass (coefficient of variation $= 70$ %). The relationship between annual production (P) in g DW

Table 1. Data sets used to assess the biomass variability and timing of peak biomass of seagrass communities

Species	Lat.	Location	Source
Cymodocea serrulata	27°S	Australia	Boon (1986)
Cymodocea nodosa	41°N	Spain	Perez & Camp (1986)
Enhalus acoroides	9°S	Papua-N. Guinea	Brouns & Heijs (1986)
Halophila decipiens	17°N	Virgin I.	Williams (1988)
Halodule wrightii	26°N	USA	Morgan & Ketting (1984)
Heterozostera tasmanica	38°S	Australia	Bulthuis & Woelkerling (1981)
Posidonia oceanica	43°N	Spain	Romero (1985)
Posidonia oceanica	40°N	Italy	Ott (1980
Ruppia megacarpa	35°S	Australia	Lukatelich et al. (1987)
Ruppia sp.	41°N	Spain	Perez & Camp (1986)
Syringodium filiforme	28°N	USA	Gilbert & Clark (1981)
Thalassia testudinum	30°N	USA	Iverson & Bittaker (1986)
Zostera capricorni	27°S	Australia	Boon (1986)
Zostera marina	37°N	USA	Heck & Orth (1980)
Zostera marina	37°N	USA	Heck & Thoman (1984)
Zostera marina	44°N	USA	Kentula & McIntire (1986)
Zostera marina	37°N	USA	Orth & Moore (1986)
Zostera marina	53°N	England	Wyer et al. (1977)
Zostera marina	56°N	Denmark	Sand-Jensen (1975)
Zostera marina	52°N	Netherlands	Nienhuis & DeBree (1980)
Zostera marina	56°N	Denmark	Wium-Andersen & Borum (1984)
Zostera marina	37°N	USA	Adams (1976)
Zostera marina	37°N	USA	Penhale (1977)
Zostera marina	52°N	Netherlands	Nienhuis & Caperon (1986)
Zostera marina	44°N	Canada	Robertson & Mann (1984)
Zostera noltii	41°N	Spain	Perez & Camp (1986)

Table 2. Data sets used to assess daily [P/B (d)], and annual [P/B, (yr)] production/biomass balances of seagrass communities

Species	Lat.	Location	P/B (yr)	P/B (d)	Source
Zostera marina	40°N	USA		X	Dennison & Alberte (1985)
Zostera marina	40°N	USA		X	Dennison & Alberte (1986)
Posidonia oceanica	35°N	Italy		X	Drew (1978)
Zostera marina	44°N	USA	X	X	Kentula & McIntire (1986)
Zostera marina	41°N	USA		X	Thorne-Miller & Harlin (1984)
Enhalus acoroides	9°S	Papua N. Guinea	X	X	Brouns & Heijs (1986)
Thalassia hemprichii	9°S	Papua N. Guinea	X	X	Brouns & Heijs (1986)
Posidonia oceanica	43°N	Spain	X	X	Romero (1985)
Posidonia oceanica	35°N	Italy		X	Velimirov (1986)
Zostera marina	44°N	Canada	X	X	Robertson & Mann (1984)
Posidonia australis	32°S	Australia	X	X	Silberstein et al. (1986)
Halophila decipiens	17°N	Virgin I.		X	Josselyn & Fonseca (1986)
Posidonia oceanica	42°N	France	X		Bay (1984)
Thalassia hemprichii	9°S	Papua N. Guinea		X	Brouns (1985)
Thalassia testudinum	23°N	Cuba	X	X	Buesa (1974)
Zostera marina	52°N	Netherlands	X	X	Nienhuis & DeBree (1980)
Zostera marina	37°N	USA	X	X	Penhale (1977)
Posidonia oceanica	37°N	Italy	X	X	Ott (1980)
Zostera marina	56°N	Denmark	X	X	Sand-Jensen (1975)
Zostera marina	56°N	Denmark	X	X	Wium-Andersen & Borum (1984)
Halodule wrightii	26°N	USA	X	X	Morgan & Ketting (1984)
Thalassia testudinum	27°N	USA		X	Dawes & Tomasko (1988)
Thalassia testudinum	13°N	Barbados		X	Patriquin (1973)
Syringodium filiforme	27°N	USA		X	Fry & Virnstein (1988)
Thalassia testudinum	25°N	USA		X	Capone et al. (1979)

m^{-2} yr^{-1} and maximum macrophyte biomass (B) in g DW m^{-2} was best described by the relation

$$Log\ P = 1.6 + 0.32\ Log\ B \qquad (2)$$
$$r^2 = 0.24,\ p < 0.05,\ SE\ log\ estimate = 0.20$$

The relation between annual biomass and production is relatively weak (Fig. 3) reflecting variability in P/B ratios for different macrophyte communities (Fig. 4). Among the possible sources of variation in the P/B ratios of macrophyte communities I was able to test the importance of (1) differences among methods, and (2)

differences in the latitudinal position of the communities. The importance of differences in production methods was tested using analysis of covariance on the relation between annual production and maximum biomass. This analysis showed no evidence of any effect of differences in methods (F-test, $p > 0.05$) on the relation
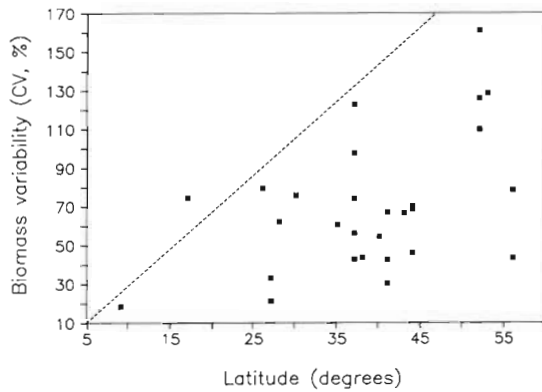
Fig. 1 Relation between degree of biomass variability (as coefficient of variation of mean annual biomass), and latitudinal position of stands. Broken line represents the suggested latitudinal-dependent boundary to biomass seasonality
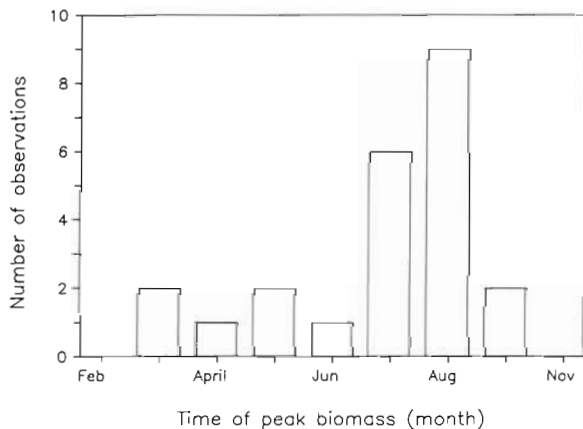

Fig. 2. Frequency distribution of the month when peak seagrass biomass occurs. June corresponds to December for southern hemisphere communities

Table 3. Mean and range for the daily and annual production rates and the maximum biomass (B_{max}) of the stands in the data set (Tables 1 and 2)

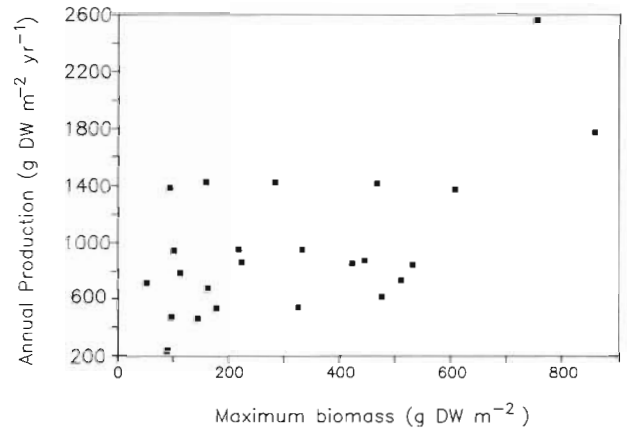| Variable	Mean	Range
B_{max} (g DW m^{-2})	315	50 – 854
Production (g DW m^{-2} d^{-1})	3.6	0.1 – 28.5
Production (g DW m^{-2} yr^{-1})	973	239 – 2557

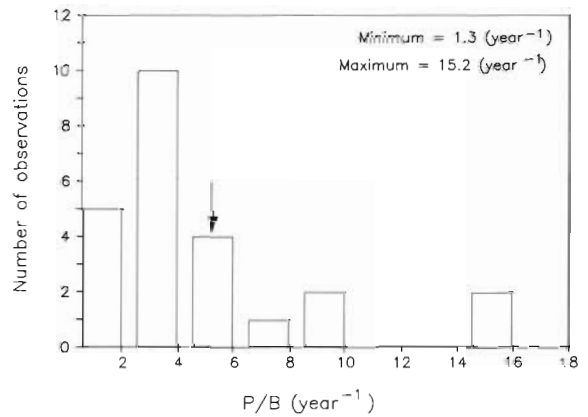Fig. 3. Relationship between maximum biomass and annual production of seagrass communities

Fig. 4. Frequency distribution of the annual production/biomass ratios of seagrass communities. Arrow indicates average ratio
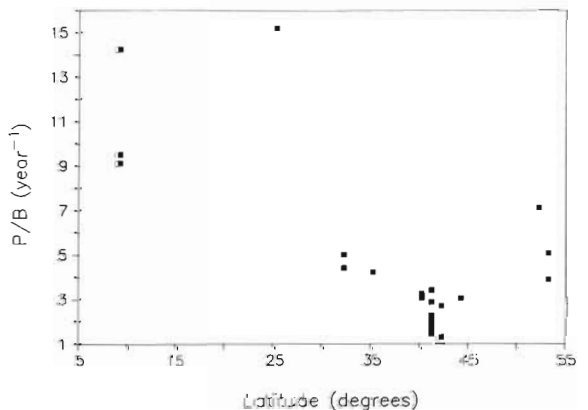

Fig. 5. Relationship between annual production/biomass ratio and latitudinal position of communities
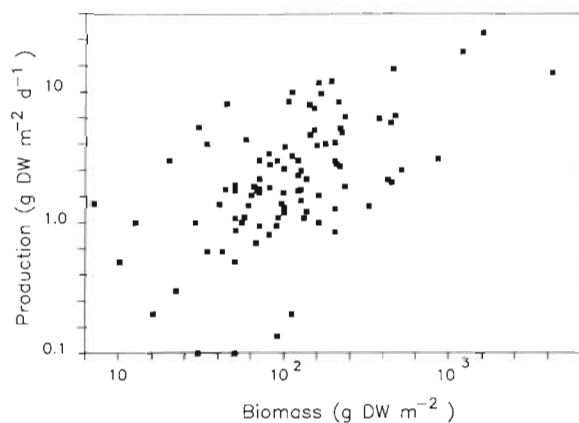
Fig. 6. Relationship between daily production rates and aboveground seagrass biomass

Fig. 7. Frequency distribution of the daily production/biomass ratios of seagrass communities. Arrow indicates average ratio

between production and biomass. The P/B ratio of the seagrass communities decreased significantly with increasing latitude ($r = -0.70$, $p < 0.01$; Fig. 5). This result, however, should be regarded as only indicative until further data on P/B ratios for tropical and subtropical stands become available. The weak relation between annual production and peak biomass was partially a result of the confounding influence of differences in latitude (partial correlation between annual production and peak biomass = 0.61, $p < 0.01$, with latitude held constant).

The relation between daily production (P_d) in g DW m^{-2} d^{-1} and biomass (B_d) in g DW m^{-2} (Fig. 6) was described by the equation

$$\text{Log } P_d = 0.60 \text{ Log } B_d - 0.89 \qquad (3)$$
$$r^2 = 0.51, \ p < 0.0001, \text{ SE log estimate} = 0.40$$

The imprecision of daily production rates estimated from areal biomass (regression error ca 2.5-fold) reflects the variability of daily P/B ratios (Fig. 7). The variability in daily biomass turnover times (5 to 666 d) appears to be unrelated to latitude ($r = 0.10$, $p > 0.05$), or to the methods used to quantify daily production (ANCOVA, F-test, $p > 0.05$). The overall variability in daily P/B was quite large (coefficient of variation = 119 %), and was partially related to temporal P/B variability (i.e. within a stand, range of within-stand coefficient of variation 28 to 116 %, average 62.6 %, $n = 6$).

DISCUSSION

Biomass seasonality

Seasonality explained a substantial fraction (average 67 %) of the biomass variability of the seagrass communities examined. This is a conservative estimate because the simple model used to assess seasonality
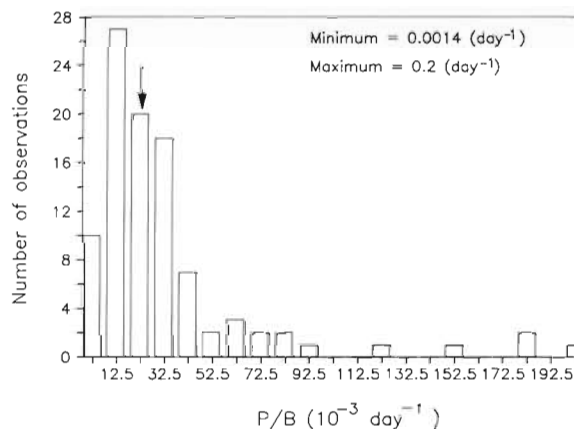
(Eq. 1) may not be equally appropriate to all seasonal responses. The importance of seasonality, however, does not imply that it is the sole source of biomass variability, since other factors (e.g. disturbance) combine with seasonal responses to yield the observed biomass variability. The extent of biomass seasonality appears to be constrained, but not determined, by the latitudinal position of the seagrass communities (Fig. 1). Thus, temperate communities often show greater seasonality than tropical and subtropical ones, but temperate communities also appear capable of displaying a wider range of seasonal responses (Fig. 1). For instance, annual and perennial forms of *Zostera marina* are known to coexist in the same coastal zones (e.g. Keddy & Patriquin 1978), and depth-related differences in the exposure to disturbance or stress often result in different seasonal responses within the same location (e.g. Robertson & Mann 1980, Williams 1988).

Patterns of biomass seasonality in seagrass communities qualitatively resemble patterns for many terrestrial plants (e.g. Lieth 1974). The seasonality of terrestrial plants also shows clear latitudinal trends (Lieth 1974), and displays a wide range of variability within latitudes (Lechowicz 1984). Similarly, the sources of variability in the seasonal response of seagrass communities growing at the same latitude may be analogous to those in terrestrial plant stands: (1) climatic (e.g. degree-days) and environmental (e.g. disturbance) differences among locations and among years (e.g. Taylor 1974, Robertson & Mann 1980, Orth & Moore 1986, Williams 1988), and (2) genetic differences among species (i.e. growth strategies; e.g. Williams 1987).

The latitude-constrained degree of seasonality in biomass has important ecosystem implications. The more constant seagrass biomass at low latitudes implies that benthic communities associated with macrophyte beds should receive a relatively constant sup-

ply of macrophyte-derived organic carbon. Similarly, the availability of substrate for epiphytic growth throughout the year must increase ecosystem primary and secondary production, and significantly influence the chemical and trophic balances of the ecosystem. On the other hand, the greater biomass variability of temperate seagrass communities indicate that their associated biota should experience considerable habitat change throughout the year.

The period of maximum biomass is rather predictable for most communities, and generally occurs (in the northern hemisphere) sometime between July and August (Fig. 2). The lack of relationship between the time when maximum biomass is reached and latitude has at least 3 possible explanations: (1) it may be that the timing of these events is determined by the occurrence of peak irradiance (Sand-Jensen 1975), which is roughly similar for all latitudes; (2) it is possible that the resolution of our analysis (month) is insufficient to detect the influence of latitude on the timing of peak biomass; and (3) it may be that sufficient variability in the timing of maximum biomass is due to differences in environmental conditions to obscure any relationship to latitude. Unfortunately, detailed data are too scarce to adequately evaluate the merits of these complementary explanations, although existing evidence suggests that both genetic and environmental control are responsible for the seasonal biomass pattern (Pirc 1986, Williams 1988).

Biomass-production relationships

Results indicate that maximum seagrass biomass is only weakly related to annual production (Eq. 1; Fig. 3). This results from the very wide variability in seagrass P/B (Fig. 5) compared to those of freshwater macrophytes (range 0.7 to 2.6, from Westlake 1982). Further, seagrass communities tend to have greater annual P/B than those reported for freshwater angiosperms (Westlake 1982). I believe that both the greater and more variable P/B ratios of seagrass communities compared to freshwater macrophytes result from growth form differences between plants inhabiting the two systems (Duarte unpubl.). Marine angiosperms cope with epiphytic accretion by sloughing off leaves after 10 to 30 wk (e.g. Ott 1980, Wahbeh 1984), thereby decreasing aboveground biomass, whereas peak biomass of freshwater angiosperms reflects better the aboveground material produced (Stevenson 1988).

Daily P/B shows considerable variation within stands and within species. The reason for this may be that daily P/B is closely dependent on the particular light conditions experienced by the stand (e.g. Kemp et al. 1987), and day-to-day variability in irradiance is likely

to be much greater than that in annual irradiance. Since tropical seagrass communities did not show greater daily P/B than those at higher latitudes, the greater annual P/B of communities inhabiting tropical and subtropical latitudes (Fig. 5) should be a consequence of their smaller biomass seasonality.

In summary, the analyses show that tropical and subtropical communities should provide a more stable habitat for associated biota than communities at higher latitudes, and at the same time should provide more organic carbon for a given structural role (i.e. greater annual P/B). The important ecosystem implications of these patterns of biomass seasonality and their influence on the balance between production and biomass enhance the need for greater research efforts directed to quantify the contributions of species-specific adaptations and environmental conditions to the seasonality of seagrasses.

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