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Productivity and Nutrient Dynamics of Tropical Sea-grass Communities in Puttalam Lagoon, Sri Lanka

Tropical sea-grass ecosystems are among the most productive submerged systems to be found. This productivity supports, through dependent species of epiphytes and associated fauna, large numbers of fish which are important protein sources for the inhabitants of tropical coastal areas. In Puttalam Lagoon, Sri Lanka, one such ecosystem, with an important fish harvest to support the coastal population, was studied in two consecutive years during the monsoon season, October 1993 and November 1994. The meadows consisted predominantly of two species of sea grasses, *Cymodocea rotundata* and *Enhalus acoroides*. Oxygen production and consumption measurements using benthic chambers placed over the sea-grass communities revealed gross production to be between 574 and 1518 g C m^{-2} yr^{-1}. All measurements showed community P:R ratios to be > 1.0, suggesting net export and/or burial of carbon in the system. The two years showed different patterns, but the variation in production rates was best explained by light penetration and salinity. Nutrient measurements showed phosphate uptake (17–82 mg P m^{-2} day^{-1}) while nitrogen fluxes displayed both release and uptake (–110 to 207 mg N m^{-2} day^{-1}). Analyses of nutrient dynamics as related to production rates indicated a dependency of the communities on sediment nutrient sources and internal nutrient recycling, despite elevated levels of water column nutrients (42–168 μg N L^{-1}, 57–184 μg P L^{-1}). Production levels were low compared to other similar ecosystems and this is thought to be due to factors including dense epiphytic growth and high water turbidity resulting from the high nutrient levels, and seasonality.

INTRODUCTION AND BACKGROUND

Sea grasses consist of twelve genera (~50 species) of rooted marine angiosperms, which are widely distributed around the world, and are often a biotope which is heavily disturbed by natural and human-induced causes (1). Their favored habitats are mainly coastal lagoons and estuaries where water movement is limited (2). Being rooted, sea grasses are able to inhabit, and thus stabilize, sandy substrates and, in addition, their roots enable them to exploit the generally higher nutrient levels found within the sediments; nutrients which are often unavailable to other primary producers in the ecosystem (3). Prior research has established the importance of sea-grass meadows to shallow coastal and estuarine ecosystems (4; and references cited therein), with sea grasses representing one of the largest contributors of fixed carbon, a source of secondary production via, for example, the associated herbivores. Sea grasses also create congenial conditions for a number of dependent organisms. Through their high productivity, sea grasses build up large carbon reserves which are utilized in the tropics by herbivores such as turtles, birds and marine mammals (5). However, it is estimated that only about 10% of the sea grass production is used by herbivores (2) and that only 1–2% of the fixed organic carbon leaches out into the water (6, 7); the main part being degraded *in situ*. Accordingly, the detrital food web is usually considered to be the primary pathway of energy flow from sea-grasses (8–10).

Sea-grass beds have long been attributed with being feeding grounds and nurseries for a wide range of species. In Puttalam Lagoon, the seagrass beds support a major fishery for the adjacent human communities. Photo: M. Richmond.

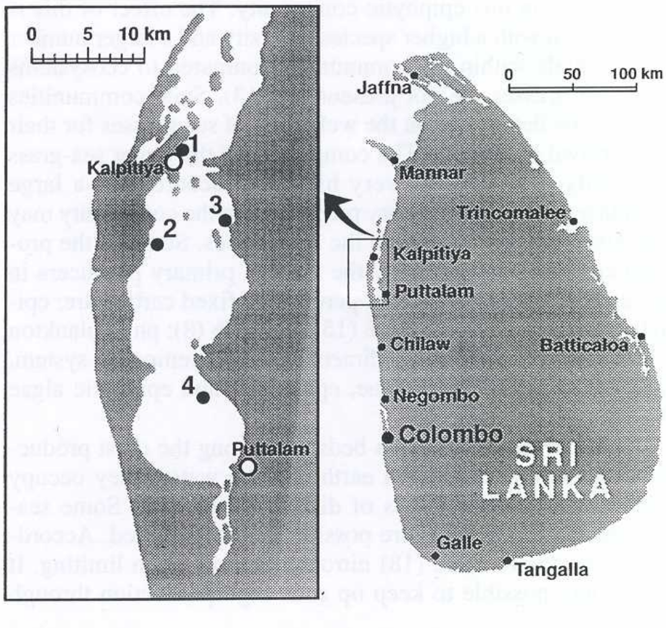
Another factor which makes sea grasses important in coastal ecosystems is the fact that the sea grasses also provide an extensive area for epiphytes to utilize as living space. In line with this, it has been proposed that the largest supply of organic carbon to higher trophic levels does not come from the sea grasses themselves, but from this epiphytic community (11). Many species of prawns and fish use the sea-grass meadows as nurseries and, even as adults, are dependent on sea grasses for the food they supply via this epiphytic community. The effect of this is an ecosystem with a higher species diversity and a larger number of individuals within the community, compared to ecosystems where sea grasses are not present (12, 13). Such communities thus become dependent on the wellbeing of sea grasses for their own survival or success. The complexity of the larger sea-grass community can, thus, be very high, and accordingly a large percentage of the total primary production in the community may come from species other than the sea grasses. Some of the proposed contributions made by the various primary producers in such an ecosystem in terms of percentage fixed carbon are: epiphytes; 46–60% (14), 48–56% (15); 22–65% (8); phytoplankton 8–72% (14); plankton and sediment algae in a temperate system, 36–45% (16); and macroalgae, epibenthic and epiphytic algae 40–90% (17).

Notably, tropical sea-grass beds are among the most productive submerged biotopes on earth, yet the waters they occupy typically contain low levels of dissolved nutrients. Some sea-grass meadows are therefore possibly nutrient limited. According to Yamamuro et al. (18) nitrogen is most often limiting. It is then only possible to keep up such high production through efficient nutrient cycling and tightly linked trophic pathways. While the sea grasses themselves take a proportion of their nutrients from the sediments, the epiphytic communities and the other dependent species are more directly dependent on water-column nutrient supply. This is noteworthy because it has been shown in several studies in eutrophic waters that sea grasses are unable to keep up with epiphytic overgrowth (8, 19, 20). This can cause a general decline in production and sometimes even the death of the sea grasses; this decline in production is partially explained by light reduction due to shading by epiphytes and phytoplankton. Under such conditions, the relative contribution of epiphytes and plankton to production grows even greater.

In Sri Lanka, there are many shallow coastal waterbodies which contain sea grasses, and which are important for the adjacent human populations.

A large proportion of the population in Sri Lanka is dependent on the marine environment for natural resources such as food and raw materials and, due to their religious background (69% Buddhists and 15% Hindus), the majority of Sri Lankans prefer fish to meat (21). As in many other tropical countries, population densities along the coast are much higher than the national average; ranging between 487 and 2600 people km^2 on the coast compared to 230 people km^2 further inland. Combined with a mean population growth of 1.5% per year for 1980 to 1990 (22), the coastal ecosystems have come under increasing stress. In particular, the shallow nearshore coastal areas such as lagoons and coral reefs, which yield some 95% of the fish catch taken each year, are showing signs of significant disturbance under human activity (23). As mentioned above, lagoons and other sheltered embayments are favored sites for sea grasses as well as for human settlements and activities. While some data areavailable on fish populations and catch rates in such places, only limited data are available on the primary production which may support them and the factors controlling this primary production. The present study focuses on one such tropical lagoon in the northwest of Sri Lanka; Puttalam Lagoon. As is characteristic of Sri Lankan waters, this lagoon is heavily fished and it supports a large human population. Catches include varieties such as rockfish, milkfish, grey mullet, crabs and several species of prawns (21). Many fishermen are specialized in lagoon fishing, while others only fish there when the ocean is rough during the monsoons. Also, fishing intensity has increased in the last years due to relocation of people from the north as a result of civil strife.

Figure 1. Map of Sri Lanka and Puttalam Lagoon showing the location of the different study sites.



Like many tropical lagoons, Puttalam Lagoon has a well-developed sea-grass community, and given the extensive fishery, sea grasses are likely to play a considerable role in supporting local fisheries production; the extent of this is not yet known. The two most common sea-grass species found in Puttalam Lagoon are the Round-tipped Sea Grass, *Cymodocea rotundata*, and Tropical Eelgrass, *Enhalus acoroides*. These are pioneering species typical for the tropics (19) and are common in the Indian Ocean (12). The meadows they form in Puttalam Lagoon are most often dispecific, however, other species are found in the lagoon including *Thalassia hemprichii*, *Halodule uninervis* (both the wide- and narrow-leaf varieties), *Syringodium isoetifolium*, *Cymodocea serrulata*, *Halophila ovalis* and *Halophila decipiens* (24).

Given that the main factors controlling seagrass community productivity in tropical ecosystems are light, temperature, salinity, and nutrient availability, (1, 3), the present study set out to quantify sea-grass productivity in the lagoon and to determine which of the above factors are likely to be controlling it.

MATERIALS AND METHODS

Study Site

The study was carried out in Puttalam Lagoon, Sri Lanka (Fig. 1), at the beginning of the northeast monsoon in mid-October, 1993, and in November 1994. The lagoon covers approximately 400 km^2 and is very shallow with depths between 1 and 2 m and a central furrow with a depth of approximately 5 m. The salinity of the lagoon ranges from oceanic levels in the northern mouth to hypersaline in the south. The coast is fringed mainly by mangroves, marsh and some coconut plantations, as well as aggregations of shrimp farms in some areas. The shrimp farms release their effluents into the lagoon, which contains not only shrimp excrements but also a number of chemical agents used in shrimp farming.

Four study sites were chosen at different locations within the lagoon; Site 1 at the mouth of the lagoon outside the village of Kalpitiya where the conditions are ocean-like; Site 2 and Site 3 in the middle basin; and Site 4 outside the village of Puttalam in the innermost basin (Fig. 1). The water depth where the measurements were carried out was ~1.1 m at all sites. No sea grasses were found at Site 4 in the second year so this site was excluded from the 1994 analyses.

Community Production Measurements

Given that the rate of release of oxygen during photosynthesis is directly proportional to the rate of carbon fixation the method used here monitored the rate of oxygen release from the sea-grass community and then calculated primary production. It should be noted, however, that the measurements taken represent the total community entrapped under the benthic chambers, including the various epiphytes and the associated fauna. Thus, the measurements are of community production. There has been some discussion as to whether this method gives an underestimation of the primary production because oxygen may be transported to the roots and, therefore, there is the possibility of oxygen storage. Also, factors such as photorespiration, leakage of dissolved organic carbon, and the formation or translocation of carbon reserves may cause a discrepancy between net photosynthesis and actual growth (1). However, the method has been demonstrated to give a good estimate with a possible underestimation in the order of 10–15% (3, 24, 25).

Two different production values are obtained from the method. *Gross community production*, which is the total amount of organic matter produced by the communities' photosynthesizing members, and *net community production*, which is gross primary production minus organic material used by community

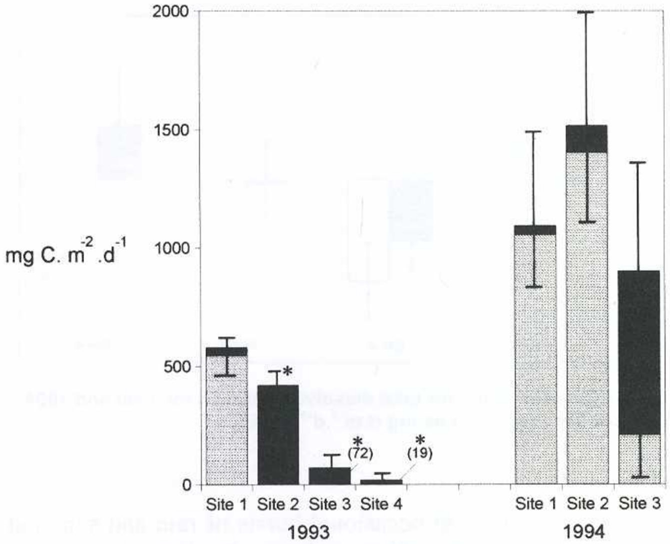


Figure 2. Gross community production for each site in Puttalam Lagoon with standard error bars. Data denoted with an * are without respiration data and SE bars are given above for net production, and below for respiration. n = Net production. o = Respiration.

inhabitants in respiration. Thus, net production represents the amount of resource which may be utilized by other organisms. For the sake of comparing different sites, this balance between production and respiration can also be expressed as the P:R ratio so that communities with P:R > 1 are said to be autotrophic (*in situ* production above *in situ* demand), or heterotrophic with P:R < 1 (*in situ* demand exceeds *in situ* production).

Measurements were carried out by using four replicate watertight plexiglass domes built as taller and somewhat more automated replicas of those described by Johnstone, Koop and Larkum (27) (Fig. 2). These were placed over the sea-grass communities at each site and anchored by pushing them 5 cm into the sediments to prevent dome movement and water exchange under the dome edge. Each dome had a volume of 216 L with a basal area of 188 cm^2. The water inside was stirred by an Attwood Miniking 360 pump, pumping at a speed of approximately 600 L hr^{-1}. This speed was chosen because preliminary dye tests showed this to best simulate the ambient water mixing rate. In addition, the different sea-grass communities examined had approximately the same structure, with 90% of the sea grasses represented being a mixture of *Cymodocea rotundata*, and *Enhalus acoroides*. The ratio between these two was generally 30% *C. rotundata* and 70% *E. acoroides*, and benthic coverage at all locations was approximately ≥ 90 to 95%.

Sampling was done at different time intervals for the different parameters over a period of six hours each sampling day. Oxygen and temperature were measured every hour through a resealable port in the dome using a WTW Oximeter 191. Because of a local night curfew, respiration was carried out during the day by measuring oxygen uptake in the domes covered with black plastic. It was then assumed that respiration by the community in the dark was the same as the respiration in the light (28). All oxygen values were converted to carbon equivalents using a conversion factor of 0.31 (29). As a control for water column activity, a water column sample of 2 L was enclosed in a flask at the beginning of the experiment and this was monitored for changes in oxygen concentration. The flask was incubated *in situ* and the production or consumption obtained was subtracted from the dome data.

Nutrient and Salinity Measurements

In addition to primary production measurements, water samples for nutrient and salinity analyses were taken from each dome every second hour using a 50 ml syringe and needle pushed through self-sealing sampling ports on the side of the dome. An equal amount of water was allowed to enter the dome through a similar needle and port on the opposite side of the dome. This prevented interstitial water (with another nutrient concentration) from being drawn from the sediment. Samples were also taken from the water adjacent to the domes for ambient nutrient determinations. All samples were immediately put on ice for transport to the research station to be frozen until analyzed, and all nutrient analyses were carried out according to standard methods (30, 31). Flux rates were determined by plotting the change in concentration over time for each dome and nutrient, and then applying a linear regression to the data (least square method); the slope of this curve was taken as the rate of release or uptake. The rates for each site were then averaged and the standard deviation calculated. A water-column control was conducted, as for oxygen measurements, as a check on water-column nutrient regeneration. Water-column values were subtracted from dome values to give the flux component that was due to the benthos.

Light conditions at each site were measured every hour for the same six hours, using Secchi disks of different colors. Salinity was measured with a Meiji Techno Salinometer S-1. The data for each site was averaged over the time of incubation.

The data collected was analyzed statistically using a range of methods. These included linear regression, multiple linear regression, two-factor ANOVA with replication and single factor ANOVA. Cochran's test of variance homogeneity was used to test if ANOVA was applicable. Student-Neuman-Keuls among means comparison was used to separate sites when significant difference was shown by the ANOVA. Where p values are given, the method used is a single factor ANOVA unless otherwise stated; n = 4 for all analyses from 1993, and n = 3 for all analyses for 1994.

Mapping Sea-grass Distribution

Sea-grass distribution within the lagoon was determined by conducting parallel transects laterally across the lagoon with a seperation of 250 m and a sampling frequency of 100 m until the border of a sea grass was encountered. The borders of a sea-grass area were better defined by a 20 m sampling frequency. Transect and sampling point location were determined using a Garmin 75 GPS which proved to have a mean accuracy of ± 20m; which was consistent on a given day. The data obtained from the transects was plotted and used to produce a map of sea-grass distribution within Puttalam Lagoon.

RESULTS

Community Production

Results from the dissolved oxygen measurements showed a net production of O_2 at all sites. The carbon fixation calculated from the oxygen data showed there to be some variation in net community production within years and a two-factor ANOVA with replication gave a significant difference between years (Fig. 2). In the first year, Site 2 had the highest mean value with the other sites having a similarly lower value (Fig. 2). This difference in net production between the sites was significant ($p < 0.001$). The net production observed at each site in the second year could not be separated statistically.

Unfortunately, due to a five o'clock curfew in 1993, respiration could only be measured at one site, Site 1. The respiration value obtained showed that respiration was a large component of the total O_2 budget compared to net production and the resulting P:R ratio was only marginally above one (1.03). The data from the second year show that the respiration value from the first year was within the correct range and the P:R ratios from the second year were between 1.04– 4.3; with Site 3 having the highest value. Since net production was positive at all sites, the P:R ratios for all sites were above one indicating a potential net export and/or burial of carbon in the system. Further, the estimated gross production values were within the range reported elsewhere for similar ecosystems (17, 26, 28).

Dissolved Nutrient Standing Stocks

Results from nutrient analyses showed there to be considerable variation in the total concentration of both dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP). In 1993, the ambient water-column concentration of total DIN at Site 4 was lower than for the rest of the sites ($p < 0.05$; Table 1), whereas the values from 1994 showed no statistical differences between sites. The largest nitrogen stock at all sites existed in the form of ammonia, which occurred in high concentrations (22–135 $\mu g\ N\ L^{-1}$), while there was less nitrate and nitrite (5–43 $\mu g\ N\ L^{-1}$). As shown in Table 1, ammonia levels played the greatest role in altering the total DIN levels observed and in 1993 they accounted for the difference in nitrogen levels between Site 4 and the others.

With regard to phosphorus, statistical analysis of the 1993 data showed the mean concentrations from Sites 1 and 3 to come from phosphate pools with the same means (Table 1), while Site 2 had significantly lower and Site 4 significantly higher phosphate concentrations ($p < 0.05$). There were no statistical differences between sites in 1994.

Community Nutrient Fluxes

Nutrient fluxes showed considerable variation for years and exhibited both uptake and release from the benthos. The difference in nitrogen and phosphate fluxes between the sites was not statistically significant, however, phosphate uptake decreased the farther into the lagoon one got (Figs 3 and 4). The phosphate fluxes corresponded to the nitrogen fluxes except in Site 1 where there was a large uptake of phosphate but a small uptake of nitrogen. The phosphate fluxes 1994 showed heteroscedastic variances in the Cochran's test, even after logarithmic transformation, and were therefore not statistically separable.

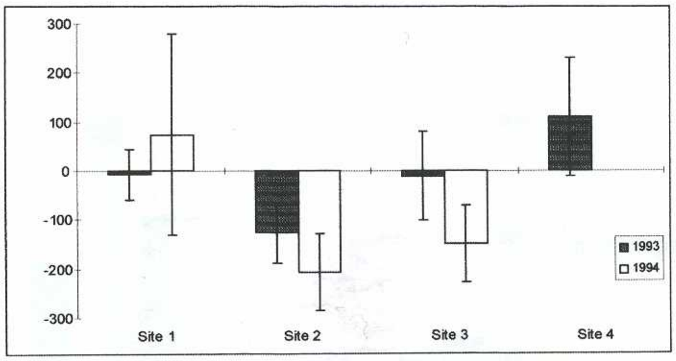


Figure 3. Benthic fluxes for total dissolved nitrogen for 1993 and 1994. Flux rates are expressed as mg N m^{-2} d^{-1} (± SE).

Light, Temperature and Salinity

One of the other physical parameters measured at each site was light penetration, which showed some differences between sites. In 1993, light penetrated deeper at Site 2 and Site 4, than at Sites 1 and 3 ($p < 0.001$) while in 1994, the best light penetration was found at Site 3 compared to the other sites ($p < 0.002$; Table 1). Light penetration was, however, poor overall.

Salinity values showed both a site and yearly difference. In 1993, at the innermost site, Site 4, was hypersaline with lower values observed at the other sites ($p < 0.001$; Table 1). By comparison, in 1994, Site 3 had a significantly lower salinity than the other sites ($p < 0.002$) Weather during this sampling period was partly cloudy with occasional bursts of rain and sun, and this may have had some effect on the results obtained.

For both years the water temperature showed a slight increase every day, never going below 28°C in the morning and never above 31°C in the afternoon.

Seagrass Distribution

The results of the transect work showed the seagrasses to be widely distributed throughout the lagoon and it confirmed that the majority of the seagrass beds were essentially dispecific, being comprised of the Round-tipped Sea grass, *Cymodocea rotundata*, and Tropical Eelgrass, *Enhalus acoroides*. Further, digitizing and mapping the data showed the seagrasses to represent approximately 23.88% of the total lagoon area; 54.9 km^2 of a total area of approximately 230 km^2 (Fig. 5).

DISCUSSION

As mentioned in the introduction, the major aims of this study were to determine the role of the major physicochemical parameters of Puttalam Lagoon on sea-grass community production, and to see if community production varied spatially throughout the lagoon.

The results obtained showed a clear variation in production between communities (Fig. 2) but this variation was not directly explainable by ambient nutrient concentrations alone. The community production recorded for all of the study sites was within the range reported in the literature for similar sea-grass communities, however, the values observed were at the low end of the reported range (Table 2). While it is considered here that this may be due to natural variation between ecosystems, the results also suggest that in Puttalam Lagoon it may in part be due to human input.

One factor that is likely to play an important role in determining community production levels is nutrient availability; primarily nitrogen and phosphorous (18). A comparison of the data obtained here showed no significant correlation between water-column nutrient concentrations and community production despite the fact that there were high levels of both dissolved inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP) at all sites (Table 1). Further, flux measurements showed there to be an active uptake of both DIN and SRP at all sites with the one correlation between uptake and production occurring at Site 2, which had both the highest uptake of DIN and the highest community production (Figs 2 and 3). Despite its location outside the major town of Puttalam, Site 4 had the lowest ambient concentrations of SRP and DIN; Puttalam town re-

Table 1. Physicochemical parameters at each study site for 1993 and 1994. The values given are means (n = 4). Those in parentheses are standard deviations.

Site	Ammonium $\mu g\ L^{-1}$	Nitrate + Nitrite $\mu g\ L^{-1}$	SRP $\mu g\ L^{-1}$	Salinity (ppt)	Light Penetration (cm)
1993					
1	128.5 (4.2)	19.9 (6.5)	164.5 (18.7)	24.9 (1.5)	56.4 (6.3)
2	128.9 (8.2)	39.5 (1.9)	102.4 (12.9)	29.6 (1.6)	96.4 (9.5)
3	120.7 (5.5)	42.4 (2.0)	151.3 (7.2)	23.6 (1.8)	41.5 (18.7)
4	42.2 (3.2)	13.9(1.0)	182.1 (13.5)	39.6 (1.0)	90.0 (16.3)
1994					
1	134.9 (5.8)	5.0 (2.1)	72.3 (21.8)	24.5 (1.2)	76.0 (5.5)
2	22.1 (1.3)	43.2 (2.5)	67.6 (23.9)	25.4 (0.8)	80.0 (8.2)
3	47.2 (1.5)	40.1 (12.8)	57.2 (14.2)	22.2 (2.9)	58.0 (4.5)

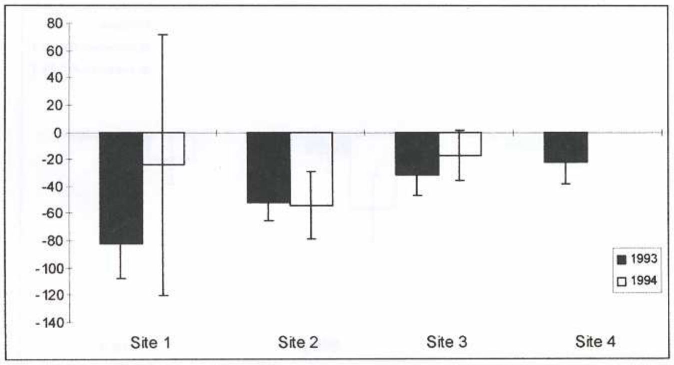
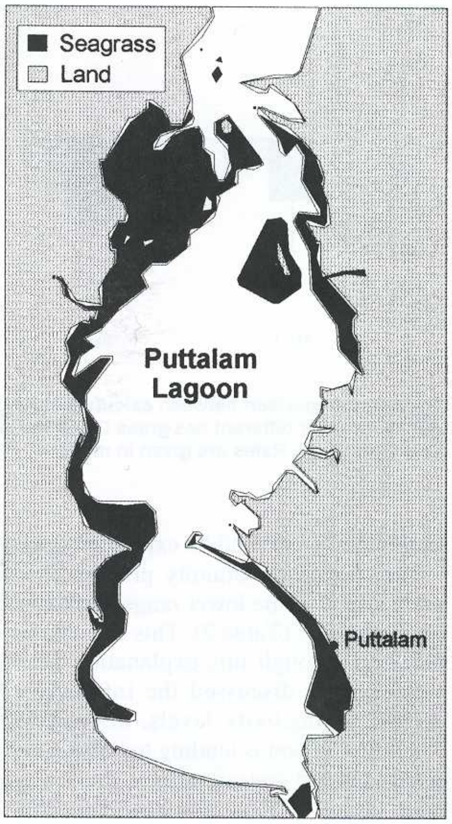


Figure 4. Benthic fluxes for soluble reactive phosphorus for 1993 and 1994. Flux rates are expressed as mg P m^{-2} d^{-1} (± SE).

leases a large percentage of its sewage directly into the lagoon. However, even the lowest ambient concentrations observed were relatively high for tropical ecosystems (32), and so it appears that the sea-grass communities are not nutrient limited at any of the sites studied.

Another important factor to be considered is the light available for the communities, as this has been shown to be a crucial factor in ecosystems with high nutrient loads (8, 19, 20). The best light penetration for all wavelengths was observed at Site 2 and Site 4 in 1993; and Sites 1 and 2 in 1994. In 1993, however, Site 4 did not have as high primary production as Site 2, and in 1994 no difference in production could be found. A factor which could explain this difference in 1993 is the initially low concentration of nitrogen at Site 4 but, as discussed earlier, no communities show a lack of nitrogen. On the contrary, the benthic community at Site 4 was also releasing nitrogen to the surrounding water (Fig. 3). Site 4 did, however, have higher salinity levels than all other sites, and this has been shown in other studies to negatively influence production rates (4, 33). The primary factors directly affecting primary production in the Puttalam Lagoon sea-grass communities in 1993 appear, therefore, to be light penetration and salinity levels, giving higher production where turbidity and salinity are comparatively lower (Fig. 6). Multiple linear regression gives the relationship; *Production (g C m^{-2} yr^{-1}) = 673 + 10 Light (cm) – 24* x *Salt (ppt)*, (adjusted R^2 = 0.601, $p < 0.0016$). The light conditions themselves may on the other hand be influenced by nutrient-related factors. In 1994, no significant difference in production could

Figure 5. A map of Puttalam Lagoon showing the distribution of sea-grass beds during October 1993.



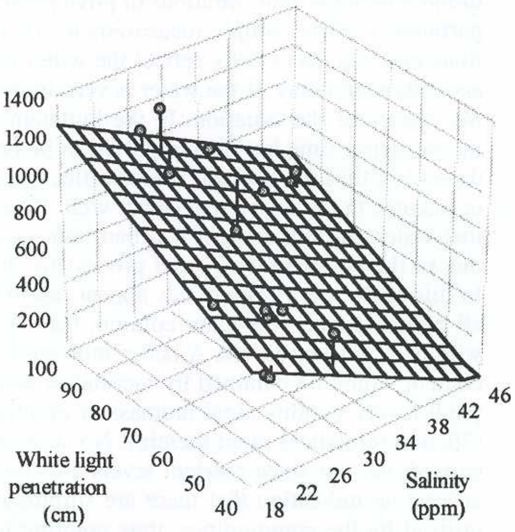


Figure 6. The relationship between light, salinity and production (Multiple linear regression gives: Production (g C m^{-2} yr^{-1})= 673 + 10 x Light (cm) – 24 x Salt (ppt), adjusted R^2 = 0.601, $p < 0.0016$.

Table 2. Examples of primary production values taken from the literature. The five top rows indicate community production and are directly comparable with each other, while the rest are sea-grass productivity, included here to give an idea of the potential contribution of the sea grass itself. Where published figures were in g dry weight, a conversion factor of 0.36 was used to convert to grams carbon, and organic (ash-free) dry weights were multiplied by 0.5. A range of values indicates multiple values.

Production C g m^{-2} yr^{-1}	P:R ratio	Species	Remark	Source
547–912	1.02–1.66	*Cymodocea rotundata* *& Enhalus acoroides*	Communities	This study
2190	1.20	*Cymodocea rotundata* *Thalassia hemprichii*	Communities	ref. 17
1460–3285	0.81–1.67	Various	Communities	
219–1752	0.94–2.25	Various	Communities	ref. 26
328–1606	0.55–1.17	Mixed species	Communities	ref. 28
182	N.A.	*Cymodocea rotundata*	Sea grass only	ref. 17
36–365	N.A.	*Cymodocea rotundata*	Sea grass only	ref. 26
1058	N.A.	*Cymodocea rotundata*	Above ground Sea grass only	ref. 28
365	N.A.	*Cymodocea rotundata*	Leaf production Sea grass only	ref. 4
150–800	N.A.	Various		
73–255	N.A.	Various	Net production, Sea grass only	ref. 2
45–1314	N.A.	Various	Leaf production Sea grass only	ref. 3

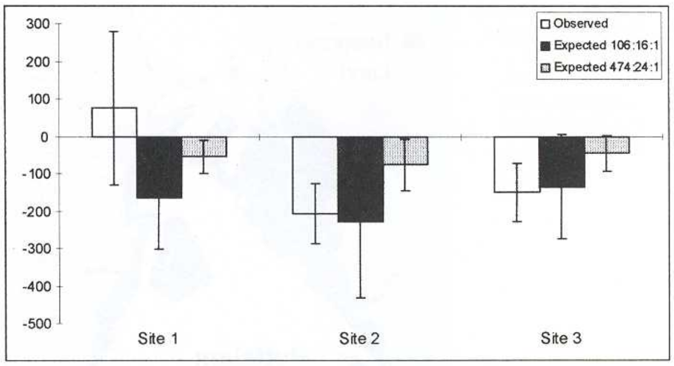


Figure 7. Comparison between calculated and observed nitrogen uptake rates for different sea grass C:N:P ratios based on 1994 production data. Rates are given in mg N m^{-2} d^{-1} (± SE).

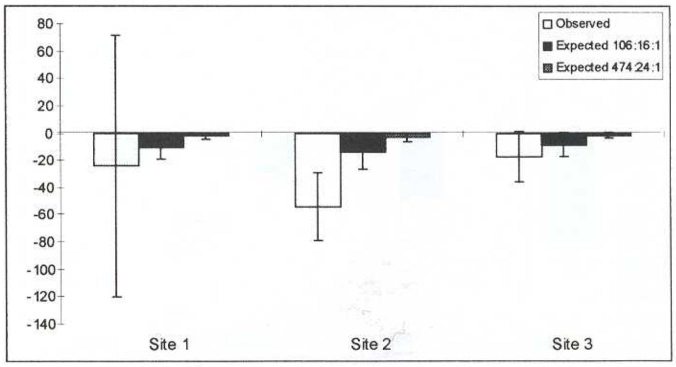


Figure 8. Comparison between calculated and observed phosphorous uptake rates for different sea-grass C:N:P ratios based on 1994 production data. Rates are given in mg P m^{-2} d^{-1} (± SE).

be found which could be explained in a similar manner.

The overall community production values observed in this study all fall in the lower range when compared to those of other similar studies (Table 2). This can also be explained by light and salinity, although this explanation needs further study. Some authors have discussed the influence of excess nutrients on general productivity levels. Several factors indicate that the Puttalam Lagoon is tending towards a eutrophic state. Ammonia occurs in high concentrations, the sea grasses are covered with thick layers of algae and cyanobacteria, and the water is very turbid with large concentrations of phytoplankton and suspended particles. Clearly, simple measurements of nutrient concentrations may not necessarily reflect the wider nutrient status of an ecosystem and may, if the water is very mobile, give a misleading picture of the situation. In the Puttalam Lagoon, however, the residence time has been reported to be between 20 and 100 days (34), thus the nutrient values reflect the nutrient dynamics or balance in the ecosystem rather well. It has also been argued that water nutrient content is a bad indicator of eutrophication due to the communities' rapid processing of soluble nutrients. In this study, the communities appear not to be able to remove all nutrients from the water column, leaving the water column with high nutrient levels. A better indication of system nutrient content would be obtained by measuring water-column chlorophyll levels, benthic algal biomass or epiphyte standing stocks (20, and references cited therein). No such measurements were carried out, but since nutrient levels are consistently high, it is at least an indication that there are surplus nutrients not being utilized by the communities, thus pointing to a possible effect of human input.

Another factor to be considered is seasonality. Tropical sea grasses can exhibit large variations in productivity (35), but small seasonal variations in the standing crop resulting from this production (5). *Cymodocea rotundata* has been shown to be twice as productive in the summer as in the other seasons (26). Seasonal variations can be attributed to the same factors as usual, i.e. light, temperature, salinity and nutrient availability. This study was carried out during the beginning of the northeast monsoon in October 1993 and November 1994 when light radiation is lower than usual due to cloudiness and occasional rains, and this could explain the somewhat low production observed.

The second main question posed by this study concerned the exchange of nutrients between the sea-grass communities and the surrounding water column. All sites showed considerable nutrient pools; the ammonia component was especially large. Although the nutrient fluxes did not show any correlation with the size of these nutrient pools or with production numbers, the largest nitrogen uptake was observed at Site 2 which had the largest production in both years. The fluxes of nitrogen and phosphate corresponded to each other except in the case of Site 1, 1993, where the phosphate uptake was larger than would be expected. No consistent pattern in the appearance of the fluxes could be found, except that variation was large and that uptake and release could be observed at all sites.

One approach to analyzing community nutrient cycles is to examine the nutrient content of the included organisms, i.e. the carbon:nitrogen:phosphate (C:N:P) ratio, and then from the production numbers derive the required intake of P and N to drive the system. As has been discussed in the literature (36), the average C:N:P atomic ratio for organisms in the sea is expressed in terms of the "Redfield ratio" of 106:16:1. On further analysis the median ratio for benthic marine macroalgae and sea grasses was found to be 550:30:1. In a later review of sea grasses only (37), the median ratio was found to be 474:24:1. The investigated communities are made up of different organisms in which the sea grasses are a single vital part, but not necessarily the greatest in terms of production. Consequently, the true C:N:P ratio would probably fall in between that of the phytoplankton (106:16:1) and that of the sea grasses (550:30:1).

A calculation of the required nutrient uptake based on these C:N:P ratios shows that to keep up the production rate measured, the greatest part of nitrogen used by the communities is not taken from the water column, despite the high amount of ammonia nitrogen available (Fig. 7). The bulk of the nitrogen supplying the sea grasses is thus likely to come from the sediments whilst an amount of the "nonbenthic" derived nitrogen may come from internal recycling of nutrients within the sea grasses from older to younger parts of the plant (38), and via nutrient transfer between sea grasses and epiphytes (39). The negative fluxes observed at Site 4, 1993, and at Site 1, 1994, may be due to a range of factors including microbial processes such as denitrification, but may also be due to enhanced uptake by epiphytic organisms. Concerning phosphorus, the situation is the opposite, with higher intake than necessary to supply the primary production at all sites (Fig. 8). This loss can be accounted for by several mechanisms, such as sediment adsorption, co-precipitation with iron and manganese oxides, and hydroxides in the water column, and direct sorption to suspended clay particles and organic matter (40). The high nutrient uptake also supports the notion that a large proportion of the production is accounted for by epiphytes and phytoplankton.

Sea-grass communities are very important as nurseries, food sources and shelter (10). The Puttalam Lagoon sea-grass communities have been shown to be autotrophic at all sites (P:R > 1) and with a mean net production of 1.1 gC m^{-2} d^{-1}, their total area represents approximately 206.4 tonnes C yr^{-1}. Given the work of Dayaratne et al. (40) it is clear that the Puttalam Lagoon fishery is highly productive and is of great significance for the adjacent communities. Although further work is required before a fully accurate estimate can be made, it is clear that the sea grasses make a significant contribution to this production.

The lagoon system, however, shows some signs of being eutrophic; ammonia occurs in very high concentrations, the sea grasses are overgrown with thick layers of algae and cyanobacteria, and the water is very turbid with large concentrations of phytoplankton. This can be one factor for the somewhat low production measurements, compared to other similar ecosystems. The lagoon ecosystem presently appears to cope with the elevated levels of nutrients, but it is unclear as to whether it would tolerate further elevation of dissolved nutrient levels. Given the relative low production observed and the apparent involvement of epiphytes and turbidity, it may be that the seagrass communities are presently at their upper threshold for nutrient loading. In the long term, such stress may cause severe deleterious effects. As discussed by Shepherd et al. (19); Tomasko and Lapointe (20); and Pollard and Kogure (8), for example, such a scenario is not uncommon or unlikely. As presented by Corea et al. (41) one source of nutrients in the southern Puttalam Lagoon is the various prawn farms. In the light of these two studies, consideration should be given to controlling the release of effluent material from these farms and the surrounding villages. Also, the release of nutrients should be monitored together with nutrient concentrations throughout the lagoon.

Furthermore, given the autotrophic nature of the Puttalam seagrass communities, a continuation of this work over the different seasons may permit an estimation of the significance of seagrass community production relative to fish stocks and the local fishery harvest. Dayaratne et al. (40) have highlighted the importance of the lagoon fishery for the local communities, and any loss of integrity in these sea-grass communities could have deleterious effects for both the fishery and community welfare. An enhanced understanding of the role of the sea-grass communities could thus provide a useful management tool in this very taxed ecosystem.

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