

**INTERNATIONAL SEAGRASS WORKSHOP
LEIDEN, NETHERLANDS
22-26 Oct. 1973**

**Review Paper
for the
Productivity/Physiology Working Group**

Production Ecology and Physiology of Seagrasses

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INTRODUCTION

A seagrass meadow is a highly productive and dynamic ecosystem; it ranks among the most productive in the ocean. Today we are faced with numerous studies of the productivity of seagrasses, dating back to the pioneering work of Petersen (1913), that give widely varying rates and little understanding of the driving mechanisms. In addition research has been largely confined to two species, *Zostera marina*, the temperate eelgrass, and *Thalassia testudinum*, the turtle grass of the tropics. In this paper we have attempted to summarize existing data on the productivity and standing stock of seagrasses with some view towards a global comparison of our understanding of the contribution of this system to the productivity of the sea.

The productivity of the sea, as the many expeditions since the GALATHEA have shown, consists basically of a pattern of a vast expanse of open ocean that has a low, relatively uniform primary production plus a few hot spots of extremely high production (Gessner, 1959; Ryther, 1969). These high production areas serve as the primary sites for the biological fixation of carbon that through advective processes and food webs is distributed to a much larger ocean area. Examples of the productive areas are the upwelling regions on the continental shelf, the shallow protected bays of any coast, salt marshes, sea-tree forests (mangroves) and seagrass meadows. These meadows, although more inconspicuous than many other coastal ecosystems, are extremely wide-spread throughout the world ocean and make a more measurable contribution to coastal productivity than might otherwise be imagined.

Primary production in a seagrass meadow is extremely complex and contributes some unique problems to the measurement of marine productivity. All components of the total productivity must be measured fully to estimate the magnitude of the productivity of the system. This includes benthic algae, epiphytic algae, and phytoplankton as well as the seagrasses. Each of these components requires special techniques that vary considerably in complexity from the now routine measurement of phytoplankton productivity to the still experimental and extremely difficult measurements of seagrass plants and their associated epiphytic flora. In spite of considerable sophistication in chemical methods our knowledge of seagrass productivity has not advanced much beyond what Petersen learned more than 60 years ago.

If little has been learned about the productivity of seagrass ecosystems in nature even less is known about the dynamics of productivity, the driving forces and mechanisms. Obviously light and temperature are major factors in controlling photosynthesis but the relationships are poorly defined and we would have little success today in predicting growth rates of a seagrass meadow from such essentially hydrographic data. Physiological studies that give ecological insight are indeed few. Scientific knowledge today is not much better equipped to explain a "wasting disease" - that widespread disappearance of *Zostera marina* that occurred in the early 30's - than it was then.

A high productivity implies a high nutrient demand and dynamic cycling of trace metals and other compounds involved in plant growth. The physiological processes involved in the supply and cycling of elements by these plants remain to be defined, although part of the answer must lie in the capability of seagrasses, since they are rooted, to absorb compounds from the sediments. In this respect seagrasses present a system for returning nutrients and other compounds to the water column that are lost to the sediments in other marine areas. It is also probable that a seagrass meadow can function as a filter and effectively trap materials from the water column.

In this review we have tried to examine the literature on all of these problems and give the reader our version of a critique of existing data, however we can tell you now that the conclusion for most of these problems is that our knowledge is in fact minimal.

STANDING STOCK AND PRODUCTIVITY

Comparative criteria and units. Westlake (1963) set standards for comparisons of plant productivity and we have in general followed his procedures. In this paper all standing stock data are presented in terms of grams dry weight per square meter (g dry/m^2). Biomass data originally presented in terms of wet weight were converted by a ratio of 10:1 which is based on experience with eelgrass (McRoy, 1970b) as well as convenience. Productivity data are generally the average rates of net production or net photosynthesis in terms of carbon fixed per unit area ($\text{g C/m}^2\text{-day}$) or per unit weight (mg C/g dry-h) presented in the literature in units of dry weight, oxygen production or more rarely carbon fixation. Herein dry weight data have been converted to carbon, following Westlake, by a proportion of 38% since data available on eelgrass indicate an organic weight of about 80% of the dry weight 47% of which is carbon. Rates presented in terms of oxygen production were converted to carbon fixation by assuming a photosynthetic quotient of 1.25, again as suggested by Westlake for natural communities growing in favorable conditions; this results in the conversion: $0.30 (\text{X mg O}_2) = \text{X mg C}$.

In cases where the original productivity data were not presented in terms of weight the rates were recalculated from the median of the range of the observed standing stock assuming a 12 hour day; these numbers are listed in parentheses in Tables 1 and 2.

As presented productivity is one specific aspect of growth. Growth, of course, can be measured in other ways such as changes in size or density. These processes may or may not also be suitable for estimates of carbon fixation. We have tried to distinguish between them here. For studies of ecosystems or biogeochemical cycles growth in terms of carbon (as an indication of energy transfer) is preferred.

Methods of productivity measurement. The seagrasses present unique problems in marine productivity measurement and a variety of techniques have been used. The rather low apparent turnover rates permit an estimate of production based on harvest of the

standing stock during the growing season (Pomeroy, 1961). Petersen (1913) estimated the production of *Zostera marina* in Danish waters by doubling the value of the maximum standing stock in late summer. Doubling was seen as a correction for leaves lost during the summer that would not otherwise be estimated in yield calculations. Grøntved (1958) however calculated production in terms of yield by subtracting the spring biomass from the summer maximum; he did not consider a correction for lost leaves to be necessary. If no other rate determining measurements are possible this harvest or yield method is useful, but the estimate must be considered a minimal estimate of net production since losses of standing stock occur that are not measured.

Changes in dissolved oxygen concentration in the water surrounding a plant have been used by several workers as measurements of the products of photosynthesis and respiration. Odum and Hoskin (1958), Qasim and Bhattathiri (1971) and Nixon and Oviatt (1972) have used an open system technique where the change in oxygen concentration in the water flowing across a seagrass meadow was used to calculate gross and net production. At first this technique appeared to be a simple *in situ* method but other workers found that estimating diffusion and mixing of oxygen across the sea surface was a complex problem and the technique has not been widely used. More often studies using a dissolved oxygen technique have relied on a closed system method where plants or parts of plants were enclosed in bottles (Jones, 1968; Buesa, 1972; McRoy, 1966, 1970b; Pomeroy, 1960) or in a type of bell jar placed directly over the bottom (Jones, 1968; Brylinsky, 1970). At the present time all measurements involving dissolved oxygen to estimate productivity must be considered questionable in view of the results of Hartman and Brown (1967) who demonstrated in freshwater aquatic plants that the oxygen resulting from photosynthesis is internally recycled in the lacunar spaces of the leaves. In eelgrass perhaps as much as 50 to 60% of the leaf volume is essentially a gas sac and presumably functions in internal recycling of gases. The validity of using changes in dissolved oxygen for productivity studies, especially in flowing waters, remains doubtful. The method surely underestimates the true rate to some unknown and possibly variable degree. This problem deserves thorough study in seagrasses. The technique, although simple, should be avoided until the consequences of internal recycling have been evaluated.

Another type of open system technique that has been applied to dense seagrass meadows in shallow waters is the use of pH and alkalinity data to calculate changes in dissolved CO_2 (Parke, Hood and Odum, 1958). This method is an improvement over O_2 techniques but is complicated by apparent disparity in the true and calculated CO_2 content from alkalinity and pH measurements especially in systems where equilibrium may not exist (Hood and Ibert, 1960).

In some more recent studies radioactive carbon (^{14}C) has been used to measure productivity directly (Dillon, 1971; Brylinsky, 1971). This method was developed for vascular aquatic plants in freshwaters (Wetzel, 1965) and can be directly applied to the seagrasses as long as the chemical differences of the water, i.e. the CO_2 system, are considered. Also few complications exist in this method. It is possible that CO_2 like O_2 is recycled in the lacunae of the leaves resulting in an underestimate of production. The magnitude of this error is unknown; it is probably much less than that of O_2 recycling. Another source of underestimation of the carbon fixation rate is the leakage of carbon that had been fixed in photosynthesis. Brylinsky (1971) found in some subtropical seagrasses that this leakage amounted to about 2% of the total carbon fixed.

A unique method of estimating production was developed by Zieman (1968) who used plastic coated staples to label the leaves just above the meristem in the leaf base. After a short time, less than 2 weeks in tropical species, the distance was measured from the staple to the meristem area. This increase in length can be related to growth, a necessity to obtain data on carbon fixation. The technique has the advantage that repeated *in situ* measurements can be made throughout the growing season. It does not provide any estimate of root and rhizome growth and requires a good unit area estimate of leaf density. Zieman and his colleagues have effectively used this in studying the effects of thermal effluents on *Thalassia* (Bader and Roessler, 1971).

COMPARISON OF STANDING STOCK

Measurements are available for only 5 species of tropical and subtropical seagrasses (Table 1) and 3 temperate species (Table 2). Observations on two species, *Thalassia testudinum* and *Zostera marina*, comprise the bulk of available data. Under optimum conditions both species can form dense, extensive meadows in shallow coastal waters which are in many ways analogous if not comparable. ~~These two species are capable of attaining very high standing stocks, over 8 kg dry/m² for *Thalassia* and over 5 kg dry/m² for *Zostera*~~ and from the available data are the seagrasses that attain the highest biomass. The mean standing stocks for the two species also fall in a similar range, especially if only the dense beds are considered; here the average seasonal maximum biomass is generally in the range of 0.5 to 1.5 kg dry/m². Of the other species that have been studied only *Posidonia* in dense meadows in the Mediterranean Sea appears to approach the biomass of *Zostera* and *Thalassia*. ~~The smaller seagrasses, such as *Syringodium* and *Halodule*, although capable of forming dense stands do not attain the high biomass of the larger meadow-forming species. These under optimum conditions have seasonal maximum standing stocks under 500 g dry/m² and average values about 100 to 200 g dry/m².~~

Although the available data for all species are scanty it appears that the high and low biomass levels correspond to the growth form classification presented by den Hartog (this volume). That is, the larger meadow forming groups, the magnozosterids and enhalids which includes *Zostera* subgen. *Zostera*, *Cymodocea*, *Thalassia*, *Posidonia*, *Phyllospadix* and *Enhalus* attain average seasonal biomass in the range of 0.5 to 1.5 kg dry/m² and the remaining groups, parvozosterids, syringodiids and halophilids, only 100 to 200 g dry/m². This generalization is not well substantiated and needs to be examined more thoroughly. It is possible, however, to make this generalization because of the wide variability associated with the measurement of standing stock. McMahan (1968) found that in a dense bed of *Syringodium filiforme* 20 standing stock samples only estimated the true mean by $\pm 30\%$ and the same number of samples in a *Halodule beaudettei* bed by $\pm 20\%$. These estimates are very similar to those in dense *Zostera marina* meadows (McRoy, 1966). Since most standing stock measurements do not involve a large number of samples the mean values in Tables 1 and 2 are probably not much better than $\pm 50\%$; this is borne out by the wide range observed within a single stand.

Table 1. Standing stocks and productivities of tropical and subtropical species of seagrasses.

SPECIES	LOCALITY	STANDING STOCK (g dry/m ²)		DENSITY No/m ²	PRODUCTIVITY		REFERENCE
		Range	Mean		(g C/m ² -day)	(mg C/g dry-h)	
1 <i>Cymodocea nodosa</i>	Mediterranean	13-342	-	-	5.4 -18.7	(0.82-2.9)	Gessner and Hammer, 1960
2 <i>Halodule beaudettei</i>	Florida	-	-	-	-	1.81	Brylinski, 1971
	N. Carolina	105-200	200	-	0.48-2.0	-	Dillon, 1971
	Texas	22-250	93	15,118	-	-	McMahan, 1968
3 <i>Posidonia oceanica</i>	Malta	543-1072	742	-	2-5	(0.21-0.52)	Drew, 1971
4 <i>Syringodium isoetifolia</i> <i>Thalassia hemprichii</i>	Laccadives	-	-	-	5.81	-	Qasim and Bhattathiri, 1971
5 <i>Syringodium filiforme</i>	Texas	29-67	45	3,099	-	-	McMahan, 1968
6 <i>Thalassia testudinum</i>	Venezuela	-	1200	-	-	-	Gessner, 1971
	Cuba	-	400	-	-	-	Murina et al., 1969
	Cuba	30-690	390	-	-	-	Buesa and Olacchia, 1970
	Cuba	200-800	340	-	9.3 -12.5	1.7 -2.3	Buesa, 1972
	Puerto Rico	-	-	-	2.4 -4.5	-	Odum et al., 1959
	Puerto Rico	538-7376	-	-	-	-	Burkholder et al., 1959
	Florida	-	-	-	3.13	-	Odum, 1956
	Florida	-	-	-	10.2	-	Odum, 1957
	Florida	-	325	-	-	-	Phillips, 1960
	Florida	20-400	-	-	5.7 -16	(2.3 -6.3)	Odum, 1963
	Florida	74-89	81	-	0.35-1.14	0.36-1.3	Pomeroy, 1960
	Florida	300-1800	835	-	0.9 -2.5	0.13-0.25	Jones, 1968
	Florida	-	-	-	1.7 -2.3	-	Zieman, 1968
	Florida	500-8100	3100	-	-	-	Bauersfield et al., 1969
	Florida	-	-	-	-	1-3	Brylinski, 1971
	Florida	-	-	-	2.8 -14	-	Thorhaug and Stearns, in press
	Texas	-	-	-	0.9 -9.0	-	Odum and Hoskin, 1958
	Texas	-	3000	-	-	-	Parker et al., 1963
	Bahamas	-	-	-	0.5 -3	-	Patriquin, 1972

Table 2. Standing stocks and productivities of temperate species of seagrasses.

SPECIES	LOCALITY	STANDING STOCK (g dry/m ²)		DENSITY No/m ²	PRODUCTIVITY (g C/m ² -day) (mg C/g dry-h)		REFERENCE
		Range	Mean				
1 <i>Zostera marina</i>	Denmark	210-487	487	-	-	-	Grøntved, 1958
	Denmark	272-960	-	-	2-7.3	(0.27-0.99)	Petersen, 1913
	England	-	120	-	-	-	Burton, 1961
	Canary Islands	70-89	89	-	0.35	(0.33)	Johnston, 1969
	Nova Scotia	785-1251	1018	-	-	-	Mann, 1972
	Massachusetts	15-29	-	-	0.04	(0.15)	Conover, 1958
	Rhode Is.	-	225	-	0.4-2.9	(0.15-1.1)	Conover, 1968
	Rhode Is.	-	100	-	2.6	(2.2)	Nixon and Oviatt, 1972
	New York	247-2062	762	-	-	-	Burkholder and Doheny, 1968
	New York	224-5157	1906	-	-	-	Wilson and Brenowitz, 1966
	New Jersey	153-593	-	-	-	-	Moeller, 1964
	N. Carolina	82-156	-	-	0.2-1.2	-	Williams, 1966
	N. Carolina	175-545	273	-	0.5-1.7	0.17-2.2	Dillon, 1971
	California	12-421	-	-	-	-	Keller, 1963
	California	6-192	-	-	-	-	Waddell, 1964
	Washington	94-539	-	-	0.6	(0.16)	Phillips, 1969
	Washington	116-231	117	151-893	0.7-4	(0.33-1.9)	Phillips, 1972
	Alaska	186-324	180	710-2101	8	0.55	McRoy, 1966
	Alaska	62-1840	1000	599-4576	3.3-3.8	0.3-0.4	McRoy, 1970a, 1970b
	Japan	70-235	-	-	-	-	Kita and Harada, 1962
	Sakhalin	31-900	900	-	-	-	Shchapova and Vozzhinskaya, 1960
	White Sea	164-203	-	-	-	-	Kuznetsov and Marveeva, 1963
	White Sea	-	-	-	-	-	Kireyeva, 1965
	Black Sea	100-150	-	-	-	-	Zenkevitch, 1963
2 <i>Zostera noltii</i>	Japan	-	-	-	-	6.4-8.4	Ogata and Matusi, 1965
3 <i>Phyllospadix scouleri</i>	Sakhalin	85-150	-	-	-	-	Shchapova and Vozzhinskaya, 1960

What controls the maximum standing stock? The maximum biomass in any seagrass meadow is related to density as a function of leaf size. This is essentially a control by light through shading. That is, there must be some density of leaves that results in increasing self-shading and becomes a controlling factor. The leaf area index (LAI) is an estimate of this maximum leaf density (Evans, 1972). In terrestrial cereal crops maximum values of the LAI are as high as 9, for broad-leaved trees in a tropical rain forest it can reach 20 (Golley, 1972). In seagrasses LAI over 20 can be attained in a dense meadow (Table 3). These very high values suggest some adaptation to the lower light levels of a submarine life; it is also possible that the highest LAI for any seagrass species can only be reached where some degree of water movement is present. The consequence of increasing the bottom area by more than 20 times is of course extremely important to other inhabitants of the community.

If density and leaf area control the maximum standing stock under favorable conditions within a growth form, then little difference would be expected between high and low latitudes. This then suggests that the similar LAI of 19 in a *Thalassia* meadow in Venezuela and that of 21 for a *Zostera* meadow in Alaska is no coincidence but should be expected as should comparable biomass values. On the other hand a similar standing stock does not necessarily reflect similar dynamics of the processes going on within the system.

Comparison of Productivity. Although similar standing stocks can be attained in seagrass meadows growing in widely different localities and environmental conditions, the ecology of this production or growth can be very different. The temperate seagrasses have a well defined growing season; for tropical or at least subtropical species the season is not well defined but net growth does not proceed during all times of the year. Net productivities in the range of 12 to 16 g C/m²-day are reported for *Thalassia testudinum* (Table 1). These are extremely high daily rates of production and rank with the highest productivities of terrestrial monospecific agricultural crops such as *Zea mays* (Westlake, 1963). The maximum daily rate for temperate seagrasses, largely *Zostera marina*, are about half those reported for *Thalassia* (Table 2) and even these rates are high enough to be in the same range, on a unit area basis, as the productivity associated with the phytoplankton community of marine upwelling region (Ryther, 1969). These data at least establish the seagrasses as one of the most productive ecosystems in the sea and the measurements still do not include the contributions of the phytoplankton, epiphytic flora and benthic algae.

Some estimates of the annual contribution of a seagrass meadow are possible from the available data. Assuming for the subtropical zones such as Texas or Florida a net growing season of 250 days and an average productivity of 4 g C/m²-day this would yield a total annual production of about 1000 g C/m²; likewise in the temperate regions where the growing season may be limited to 120 days the annual production would be 480 g C/m². These estimates are consistent with those of Dillon (1971) and Phillips (1969) for temperate *Zostera marina* beds as well as with Jones (1968) for *Thalassia testudinum* beds in Florida. Some workers have estimated much higher annual production rates by taking a mean or maximum daily growth rate and multiplying by 365. This practice is clearly unacceptable and can result in an estimate of efficiency of utilization of solar

Table 3. Estimates of leaf area index (LAI) in seagrasses.

SPECIES	REGION	LAI m ² /m ²	REFERENCE
<i>Posidonia oceanica</i>	Mediterranean	6.9 to 8.1	Drew, 1971
<i>Cymodocea nodosa</i>	Mediterranean	8 to 11	Gessner and Hammer, 1960
<i>Thalassia testudinum</i>	Venezuela	18.6	Gessner, 1971
<i>Zostera marina</i>	Puget Sound	1 to 4	Phillips, 1972
	Alaska	12 to 21	McRoy, 1970b

Bisc Bay = avg 5 max ≈ 14
measured

4000 × 10 cm × 1 cm
10 cm²/bl

4 × 10³ × 10 cm × 10 cm
1 × 10⁻³

4-8

7 × 10⁻³ × 2

radiation that is unreal for green plants. For example, Thorhaug and Stearns (in press) have calculated an annual production for *Thalassia* in Florida to be $\sim 7200 \text{ g C/m}^2\text{-yr}$ more than twice the known most productive plant community of cultivated plants in the tropics (Wetzel, 1963).

Comparison of a unit area of seagrass productivity involves numerous variables and depends on the standing stock of the stand as well as environmental conditions. A more useful way to examine the relative productivity of species is to express the rates on a weight basis. This does not do much to clarify Tables 1 and 2 but with two exceptions (Odum, 1963; Ogata and Matsui, 1965) all rates are in the range of 0.1 to 2.5 mg C/g dry-hr. The range within a species is as great as that between species and no conclusions are possible. Part of the explanation must be the differing temperature and especially light conditions during measurements.

In a few instances productivity data are available that can be expressed in relation to available light energy. In all cases these are not experimental studies in the laboratory but taken from simultaneous field measurements of growth and incident solar radiation. In Florida, Jones (1968) estimated this to be 5.3 to 10.8 mg C/m² per langley (ly) in a *Thalassia* bed or 6.4 to 13 $\mu\text{g C/g dry-ly}$ for a unit biomass. Dillon (1971) measured very similar rates of 6.61 to 9.26 mg C/m²-ly and 7.5 to 44 $\mu\text{g C/g dry-ly}$ for *Zostera* beds in North Carolina. Rates from Alaska are slightly higher: 12.9 to 14.4 mg C/m²-ly or 13.5 to 17 $\mu\text{g C/g dry-ly}$. The similarity of these values suggests a potentially useful relationship that can be used to estimate seagrass productivity. Production based on a unit of solar radiation permits the best estimate of the total annual contribution to the seagrass ecosystem. The relationship warrants better definition.

Returning to the earlier estimates for *Thalassia* of an annual production of 1000 g C/m² or about 2600 g dry/m²-yr and a standing stock in the range of 500 to 1500 indicates a turnover of 2 to 5 times per year. On the other hand in *Zostera* where the annual production is estimated to be about 500 g C/m² or 1300 g dry/m² and an average standing stock of 500 to 1500 the turnover would 1 to 3 times per year.

It remains difficult to draw conclusions about the productivity of seagrasses. With the data that are available only broad limits can be assigned to the net rates. No good comparable studies of productivity for several species of seagrasses using comparable methods are presently available.

EPIPHYTES AND BENTHIC ALGAE

Seagrasses are only one component of the primary producers in a seagrass community. Others include the epiphytic flora, that may at times be an appreciable portion of the leaf biomass, and the macro- and microscopic benthic algae. To our knowledge no single study has considered all of these components. In addition, of course, the phytoplankton of the water column contribute to the overall productivity of a seagrass meadow but this will not be considered here.

The epiphytic flora **can be** extremely diverse and include as many as 100 species of algae (den Hartog, this volume; Van der Ben, 1969; Kita and Harada, 1962). Most often this flora is dominated by a few species. The leaves of *Zostera* in Alaska are at times covered with a dense felt that primarily consists of the diatom *Ishmia nervosa*. The biomass of this epiphyte can become immense and in maximum development amount to as much as 50% of the total leaf plus epiphyte dry weight.

The initial development of the epiphytic community on *Zostera marina* has been examined in detail by Sieburth and Thomas (1973). They found few bacteria or algae on the surface of young *Zostera* leaves and suggest that it was necessary for one species of a pennate diatom, *Cocconeis scutellum*, to form a crust on the leaf surface before other species could develop. All studies indicate that epiphyte populations vary considerably between years and within the growing season (Brown, 1962; Hargraves, 1965; McRoy, unpublished). Sieburth and Hargraves (1973) noted that the fouling process on *Zostera* in the fall when the abrasive action of skim ice and waves removed the epiphytic crust.

There are few estimates of the productivity of the epiphytes. Marshall (1972) estimated this productivity of epiphytes on *Zostera* to be 20 g C/m²-yr for an area in Massachusetts. A more detailed study exists for epiphytes on *Thalassia* in Florida. Jones (1968) found considerable seasonal variation in epiphytes productivity; peak rates occurred in February and March, July and August with very low and sometimes undetectable rates of net production in the intervening times. The early peak was attributed to a spring bloom associated with the seasonal warming trend, that in July and November were blooms flowing hurricanes. He estimated average net epiphyte production in summer to be 0.9 g C/m²-day and in winter 0.2 g C/m²-day. The total annual production of epiphytes was estimated as 200 g C/m²-yr. This value is 20% of the estimated average net production of *Thalassia* in the region.

McRoy and Goering (in press) have speculated that the epiphyte load on seagrasses is inversely related to the nutrients available in the ambient water column. They found that carbon and nitrogen could be transferred from the solution surrounding the roots of *Zostera* through the plant to diatoms on the leaf surfaces. Harlin (1971) also observed the transfer of carbon and phosphorus from the leaf to an epiphyte. This suggests that the nutrient pool of the sediments is available for the growth of epiphytic flora and is a possible explanation for the heavy epiphyte loads observed on *Thalassia* in waters that contain very low or undetectable concentrations of nitrogen and phosphorus.

A few studies of seagrass production have also included the associated benthic macrophytic algae. Gessner and Hammer (1960) measured a standing stock ranging from 365 to 375 g dry/m² of *Caulerpa prolifera* that grew in association with *Cymodocea*; this was 52 to 96% of the total standing stock. Also Johnson (1969) estimated the production of mixed stands of *Caulerpa prolifera* and *Zostera marina* to be 1.1 g C/m²-day whereas single stands of *Caulerpa* were only 0.1 g C/m²-day and of *Zostera* 0.4 g C/m²-day. In Alaska benthic algae composed from 0.3 to 72% and averaged 14% of the total standing stock in *Zostera* beds (McRoy, 1970b). The amount of algae depended on the sediment types; in poorly sorted sediments the number of stones permitted attachment sites for larger seaweeds and this dictated biomass. Similarly Shchapova and Vozzhinskaya (1960) reported that algae were about 11% of the total macrophyte biomass in seagrass beds on Sakhalin Island in the Bering Sea.

It is apparent that the contribution of the benthic algae in seagrass beds is poorly known and deserves attention. The algal biomass may well depend on the homogeneity of the seagrass bed but it is likely that the less conspicuous, filamentous species of algae that are favored by the reduced turbulence of a seagrass bed have high rates of production and are an important contribution to the seagrass ecosystem.

The final component of benthic primary production in the seagrass beds, the microflora of the sediment, presents many problems to quantitative measurement and has been largely avoided. These algae are mostly confined to the upper few centimeters of sediment. Gargas (1972) found that microbenthic production decreased in *Zostera marina* beds as compared to adjacent bare sediment and suggested competition between *Zostera* and the algae for nutrients and light. The net production by the microbenthos, which was very seasonal, reached about 50 mg C/m²-day during the summer; this is about 1% of our estimate of average net production for a *Zostera* bed.

NUTRIENT SUPPLY

Complex and important interactions exist between nutrient supply and productivity. No explanation of the functioning of the productivity mechanism of seagrasses and their associated ecosystem is possible without some consideration of the supply of nutrients for growth.

Until very recently considerable argument existed in the literature over the actual site of nutrient uptake in submerged marine and freshwater vascular plants (Sculthorpe, 1967). New evidence with labeled isotopes of phosphorus and nitrogen indicates that the seagrasses are capable of adsorbing nutrients across the surface of the leaves or roots (McRoy and Barsdate, 1970; McRoy and Goering, unpublished data). The actual source in nature appears to depend on the kinetics and driving gradient forces of the specific nutrient compound. Generally, it appears that the sediments are the principal site of nutrient adsorption for most seagrasses.

Nutrient cycles in seagrass meadows are complex since the plants are able to utilize either the sediments or the water column for a nutrient source. In addition to the usual pathways of nutrients that exist in marine ecosystems evidence now exists showing that *Zostera* can pump phosphate and ammonia from the sediments through the plant and release it to the ambient water (McRoy et al., 1972; McRoy and Goering, in press). For phosphate in Izembek Lagoon, Alaska, the effect of this nutrient pump is to increase the concentration of dissolved inorganic phosphate in the water column; an effect that enhances the productivity of all primary producers in the system including the adjacent Bering Sea. The nitrogen cycle, being more complex, is not as readily studied as is phosphorus but experiments demonstrate that the pump is in effect and that ammonia absorbed by the roots of *Zostera* is in part subsequently transferred to the epiphytic flora, mostly diatoms, on the leaves (McRoy and Goering, in press). Harlin (1971) has also demonstrated a direct transfer of carbon and phosphate from *Zostera* leaves to the algal epiphyte *Sinithora naladum*.

Investigations into the source and supply of nutrients for seagrass growth suggest that the sediments and interstitial water contain a considerable reserve of phosphate that is available to the plants. Turnover times of this phosphate pool range from once or twice per year to once every several years in *Zostera* or *Thalassia* beds (McRoy et al., 1972; Patriquin, 1972). On the other hand the source of nitrogen required for the high growth rate of seagrass beds is more obscure. Patriquin (1972) estimated that only a 5 to 15 day supply of nitrogen was available in the sediments (Table 4). Other measurements suggest a similar high turnover of nitrogen and examples for *Thalassia* and *Zostera* beds are compared in Table 4. We know from kinetic studies that ammonia is the preferred form of nitrogen for *Zostera* and *Thalassia* but other forms of nitrogen, including low molecular weight organic compounds such as glycine, can also be used (McRoy and Goering, unpublished).

What processes could supply the high nitrogen demand? Patriquin and Knowles (1972) have measured high rates of nitrogen fixation associated with bacteria in the sediment surrounding the roots of *Thalassia* and *Zostera* and have suggested that this mechanism can account for the requirements of the plants. In addition nitrogen fixation by epiphytes, largely blue-green algae, on the leaves of *Thalassia* and *Halodule* has been reported (Goering and Parker, 1973). Indeed a high rate of nitrogen fixation is a convenient solution to the problem of supply but this does not appear to be generally the case. The results of Patriquin and Knowles are somewhat in doubt because of their methods and it appears that nitrogen fixation although certainly present in association with seagrasses is highly variable (McRoy et al., in press). Nitrogen fixation needs to be examined in detail during all seasons to evaluate its contribution to nitrogen supply.

At this time no conclusive answer is possible to explain apparent nitrogen deficits in seagrass beds. Since nitrogen can also be absorbed across the leaves a flow across the beds could provide large quantities of nitrogen. Other mechanisms are also possible. It is likely that the answer is a combination of mechanisms.

PHYSIOLOGICAL STUDIES

Physiological studies of seagrasses have concentrated upon responses to salinity, temperature and photoperiod. Other studies have considered aspects of anaerobiosis, water economy and carbon assimilation. Although these investigations might be regarded as exploratory, they are useful in the projection of future seagrass study. The culture methods outlined in the next section also offer clues to seagrass responses to a broad array of environmental conditions. Of the 50 seagrass species in den Hartog (1970), less than a fourth have been investigated to some extent physiologically.

Salinity tolerances. Biebel and McRoy (1971) studied salinity tolerance of *Zostera marina* from Izembek Lagoon, Alaska. They found the plasmatic resistance in a range from distilled water up to 3x seawater. In 4x seawater, leaf pieces were completely dead within 24 hr. Photosynthesis, which had its maximum in normal seawater, decreased nearly to zero in distilled water and in 2x seawater.

Table 4. Nitrogen requirements and sources of supply in beds at *Thalassia testudinum* and *Zostera marina*.

	<i>Thalassia testudinum</i> (Patriquin, 1972)	<i>Zostera marina</i> (McRoy, unpubl.)
I. Plant Requirements		
Standing Stock	~440 shoots/m ²	~1000 g dry/m ²
N Content (% dry wt)	2.3	2-3
Productivity	1.2-7.6 g dry/m ² -day	10 g dry/m ² -day
N Requirement	21-71 mg/m ² -day	200-300 mg N/m ² -day
II. Environment Sources		
A. Interstitial [N]		
Volume of Interstitial H ₂ O	6.1 µg-at N/liter	30 µg-at N/liter
Total Interstitial N	64 liter/m ²	15 liter/m ²
	5.3 mg/m ²	6.3 mg N/m ²
B. Extractable [N]		
Volume of Root Layer	28-863 µg-at/kg day	54-131 µg-at/liter
Total Extractable N	127 liters/m ²	150 liters/m ²
	340 mg/m ²	24 mg/m ²
C. N Fixation		
Epiphytes	—	0
Sediments	40 to 251 mg N/m ² -day	0
D. Water Column		
Total Dissolved Inorganic N	14 mg/m ³	14 mg/m ³

The effect of salinity as well as drying and pH on photosynthesis in *Zostera nana* in Japan was reported by Ogata and Matsui (1965). They found that photosynthesis was depressed in concentrated seawater but that it was less affected with an ample supply of carbon dioxide. Depression of photosynthesis was severe if pH was maintained on the alkaline side as in concentrated seawater.

The role of salinity in flowering of *Ruppia maritima* has been investigated. The studies of Setchell (1924) in California and Bourn (1935) and Phillips (1960) in Florida suggested that flowering is confined to lower salinities and that seeds are produced at a salinity at 28 ‰ or less. McMillan (unpublished) transplanted non-flowering plants from Redfish Bay, Texas, to a range of salinities in the laboratory. Those maintained above 30 ‰ did not flower but those at lower salinities, including tap water, produced flowers. Of the 5 seagrasses from the Texas coast, only *Ruppia* can be maintained indefinitely in tap water. Den Hartog (1970) however does not include *Ruppia* within the seagrasses.

Although the influence of a salinity gradient on flowering has not been studied in other seagrasses, flowering of *Halophila engelmanni* and *Thalassia testudinum* has been studied in the laboratory. McMillan (unpublished) reports flowering after two months in synthetic seawater (37 ‰) for both of the above species from Texas. Marmelstein et al. (1968) reported flowering of *Thalassia* from Florida in experimental cultures with a salinity of 28 to 32 ‰. Most, if not all, seagrasses may share a flowering tolerance for this salinity range. Their limits will need to be studied and compared.

McMillan and Moseley (1967) compared growth and survival of seagrasses from Redfish Bay, Texas, using increasing salinity tanks, both under outdoor conditions at Port Aransas and in growth chambers under controlled photoperiod-temperature conditions. During a 55-day test, *Halodule* leaves showed continuous height increase as the salinity rose to 72 ‰. *Thalassia* leaves showed no further height increase after the salinity reached 60 ‰. *Syringodium* reached its ultimate height at approximately 40 ‰. *Ruppia* showed a tolerance that was intermediate between *Thalassia* and *Syringodium*. *Halophila* had sporadic survival and its salt tolerance was not established in these tests.

Subsequent unpublished studies by McMillan compared *Halophila* from Redfish Bay under fixed salinities of 23, 37, 50, and 60 ‰. The plants were kept in synthetic seawater (37 ‰) for 3 weeks prior to the tolerance test. Plants at the 2 lower salinities survived for a 13-week comparison, but those in 50 ‰ did not survive past 8 weeks. Four of 6 plants survived 2 weeks in 60 ‰, but the remainder were dead by the fourth week. Plants that had survived for 13 weeks at 37 ‰ lost most of their chlorophyll within 24 h in 5 ‰ or in tap water. Those transferred to 10 ‰ had a trace of green tissue for 5 days, but those at 13 ‰ and 18 ‰ retained green tissue for a longer period.

McMahan (1968) studied the salt tolerance of *Halodule* and *Syringodium* from Lower Laguna Madre of Texas. He experimentally studied plants of *Halodule* in tap water and in a range of salinity, 3.5 to 87.0 ‰. After 6 weeks, plants were surviving from 3.5 to 52.5 ‰. *Syringodium* plants kept at 35.0, 44.0 and 52.5 ‰ died after 3 weeks at the highest salinity and were rated as not vigorous at 44.0. These tests showed a broad salinity tolerance for *Halodule* and narrower tolerance for *Syringodium*.

Thalassia and *Syringodium* from Lower Laguna Madre were compared in fixed salinities of 5, 10, 13, 18, 23, 37, 50 and 60 ‰ (McMillan, unpublished). The plants at various salinities, 10 to 50 ‰, survived for 2 weeks or more but those at the highest salinity, 60 ‰, did not survive or had only a trace of green tissue. In plants at 50 ‰ that were transferred to 5 ‰, the leaves of *Thalassia* remained green for several days but those of *Syringodium* became brown within 24 hr. The salinity tolerances of *Thalassia* and *Syringodium* are similar, but the leaves of *Thalassia* react more slowly to a rapid change in salinity.

By comparing the results from the salinity studies of Texas seagrasses, it can be seen that *Halodule*, which often is the sole occupant of shallow estuaries where salinity fluctuates considerably (Simmons, 1957), shows the broadest salinity tolerances. *Halophila*, which may occur in mixed stands with *Halodule*, shows the narrowest salinity tolerance. *Syringodium* and *Thalassia* show intermediate tolerances but are slightly different from each other. *Ruppia* was the only Texas seagrass which tolerated non-saline conditions.

Photoperiodic responses. Marmelstein et al. (1968) studied *Thalassia testudinum* from Florida under four fixed photoperiods. They demonstrated that vegetative growth and flowering was favored by intermediate photoperiods, 14 and 18 hours (h). Under 12 and 24 h conditions, the plants did not flower and the leaf production was not as great. They suggested that the Florida plants could be tentatively classified as intermediate-day plants.

McMillan (unpublished) studied *Thalassia* from Lower Laguna Madre, Texas, under 12, 14, and 16 h photoperiods. The plants were transplanted to the greenhouse in late March and kept in synthetic seawater (37 ‰). Flowers opened after four weeks under 14 and 16 h conditions only. This is probably the first report of flowering for Texas plants. *Thalassia* from Redfish Bay maintained under the above conditions did not flower.

Halophila from Redfish Bay was studied under various photoperiods, including 24 h conditions (McMillan, unpublished). Those transplanted in late January in two consecutive years produced new stems and leaves and after 2 months in synthetic seawater (37 ‰) produced flowers. Flowering occurred under 14, 16 and 24 h photoperiods but not under 12 h conditions. Both pistillate and staminate clones were used in the study. While *Thalassia* in the above studies may have produced flower primordia in the natural habitats prior to their transfer to the laboratory, *Halophila* was induced to flower entirely under experimental conditions.

Syringodium with flower buds was transferred to the laboratory in late March from Lower Laguna Madre (McMillan, unpublished). No subsequent development of flowers occurred in 12, 14, 16, or 24 h photoperiods. *Syringodium* from Redfish Bay, however, kept in aquaria during the fall and winter flowered under natural photoperiods in January. These responses of *Syringodium* suggest that its flowering in Texas during late winter and early spring possibly is induced by cooler temperatures and shorter daylengths.

Ruppia kept under various photoperiods in the laboratory has flowered in dilute seawater (McMillan, unpublished). Flowers were produced under 14, 16, and 24 h conditions but not under 12 h.

Halodule plants have been transplanted from Redfish Bay and Lower Laguna Madre to the photoperiod series at various times of the year, January, March-April, July-August (McMillan, unpublished). No flowers have been observed on any of these plants under experimental conditions or in the Texas bays. Den Hartog (1970) has cautioned that flowers of *Halodule* occur at the base of the plants and that they may be overlooked; this could indeed have happened.

Temperature responses. Temperature responses have been studied for *Zostera marina* by Biebel and McRoy (1971). These investigations compared two morphologically different forms, tidepool and subtidal, at Izembek Lagoon, Alaska. They showed that photosynthesis increased with temperature in the tidepool form up to 35°C but in the subtidal form up to 30°C only. At higher temperatures, photosynthesis declines sharply in both forms. McRoy (1966, 1970a) has attributed differences in the two types of *Zostera* bed to a temperature gradient in the two environments and showed that the tidepool beds could attain daily temperatures from 5° to 10°C above those in the subtidal area.

Biebel and McRoy (1971) also demonstrated that *Zostera* leaves of both tidepool and subtidal forms remained fresh, green, and alive after being frozen in seawater at -6°C for 12 h but were dead after a -9°C treatment. They suggest that the freezing resistance of *Zostera* is probably an ecological adaptation to periodic ice formation at Izembek Lagoon. Leaves of subtidal plants from near Friday Harbor, Washington, showed no resistance to the above freezing procedure. The frost resistance of Friday Harbor plants as well as that for plants from La Jolla, California was 1° to 2°C lower than that of Alaskan plants.

McRoy (1969) examined *Zostera* under arctic winter ice in Safety Lagoon, an embayment of the Bering Sea near Nome, Alaska. The plants were in a good vegetative condition although the water surrounding them was strongly saline and near its freezing point. The temperature was recorded as -1.8°C and the salinity 30 to 31 ‰.

Temperature tolerance of *Thalassia testudinum* has received attention from several investigators in Florida (Zieman, 1968, 1970; Thorhaug, 1971; Thorhaug and Stearns, in press). The series of investigations has studied the temperature tolerances from measurements and observations at various stations in southern Florida. The studies show that an optimum temperature for productivity is near 29°C and that the lethal limit for sustained time periods is 33 to 34°C, indicating a sub-lethal area of very low productivity between 29 and 32°C.

C₄ (Kranz) photosynthesis. Various seagrasses were included in a survey of ¹³C/¹²C ratios by Smith and Epstein (1971). They reported the following values: Texas seagrasses, *Syringodium*, -5.6; *Thalassia*, -9.3; *Halodule*, -10.9; California seagrass, *Zostera*, -10.0. These values were similar to those reported for seagrasses by Parker (1964), -6.0 to

-9.7. These low $^{13}\text{C}/^{12}\text{C}$ ratios indicate the Kranz (C_4) syndrome (Bender, 1971). The ^{13}C values of -5.6 to -10.9 are the lowest that have been reported among plants, suggesting that the seagrass may be unique in their carbon incorporation. As members of the Kranz syndrome, the seagrasses fix carbon initially into four-carbon acids--oxaloacetic acid, malic acid, and aspartic acid--and then, via the Calvin-Benson cycle, into 3-carbon molecules. The carbon-fixation pathway of the above seagrasses, and perhaps all seagrasses, is referred to as C_4 (Kranz) photosynthesis. Although many other monocotyledons as well as dicotyledons share this type of photosynthesis, most plants utilize only the Calvin-Benson cycle with the first intermediate of photosynthesis being the three-carbon phosphoglyceric acid and are referred to as C_3 (non-Kranz) plants.

The biogeochemistry of stable isotopes of carbon was studied by Parker (1964) in the seagrasses of Redfish Bay, Texas. He studied the isotopic composition of leaves and roots of *Thalassia*, and the entire plant of *Halodule* and *Ruppia*. He showed that the seagrasses contain similar isotopic composition but that sediment from Redfish Bay has a higher ^{13}C incorporation. Parker noted that two plants can grow side by side and one have approximately the isotopic composition of the bicarbonate carbon whereas the other is lighter than the bicarbonate. Although individuals of the same species showed approximately the same isotopic composition, different types of seagrass communities may have unique patterns of ^{13}C distribution.

Zostera marina was exposed to C^{14}O_2 in the dark and the incorporation of radioactive carbon was compared with that of marine algae (Joshi et al., 1962). The marine plants showed a predominant fraction of activity in the amino acids. In a saline environment, spinach leaves showed a pattern which closely resembled that of the marine plants.

Stirban (1968) studied the relationship between the intensity of chlorophyll fluorescence and the level of the photosynthetic zone in *Zostera marina*. He demonstrated an increase in chlorophyll *a* fluorescence from the apical to the basal zone although both the amount of chlorophyll *a* and its ratio to the accessory pigments decrease towards the leaf base.

Other physiological responses. Hammer (1968) included *Thalassia testudinum* and *Halophila decipiens* from the Caribbean coast of Colombia in a study of the effects of absence of oxygen. He demonstrated that various marine algae differed in their sensitivity to anaerobiosis. Some were killed after 2 h without oxygen. *Halophila* tolerated a short period of anaerobiosis, but after 24 h the plants failed to recover completely. *Thalassia*, because of the presence of air channels in the leaves, showed greater tolerance to low oxygen levels. McRoy (1969) found *Zostera* surviving in anoxic conditions under the ice of Safety Lagoon in arctic Alaska. Broekhuysen (1935) also found *Zostera* beds in the Netherlands to become anoxic at night.

Gessner (1971) studied the water economy of *Thalassia* in Colombia. He reported that the osmotic values in the leaves collected in the natural habitat were 32 atm and that the relative transpiration was 100%. He reported that all cells were plasmolyzed in

2x seawater, half of the cells were plasmolyzed in 1.5x seawater, but that no plasmolysis occurred at 1.2x seawater. He studied the leaf surface and showed that it has a thin, multiperforated cuticle which is ineffective in protecting against water loss.

The cell walls of various seagrasses, *Zostera marina*, *Thalassia testudinum*, *Cymodocea nodosa* and *Posidonia oceanica*, were compared by Gessner (1968). He demonstrated that leaf pieces that are exposed to air lose weight constantly until they are completely dry. There is no restraint to water loss. Gessner examined the leaf surfaces under both light and electron microscopes and noted that different species exhibited specific cuticle structures.

CULTURE METHODS AND TECHNIQUES

The culture techniques in Table 5 indicate that seagrasses can be studied under a variety of laboratory conditions. Although the transplanted seagrasses have been primarily from the Gulf Coast of Texas and from Florida, similar laboratory study of seagrasses from other regions appears equally feasible.

The difficulty of long-term study of seagrasses under laboratory control has been evaluated by Fuss and Kelly (1969). They attempted to maintain cultures in both outdoor and indoor conditions for a year. They reported that in indoor aquaria *Thalassia* survived only 7 months and *Halodule* 3½ months. In outdoor tanks of flowing seawater, *Thalassia* lived 12 months but few *Halodule* plants survived. Both Thorhaug (unpublished) and McMillan (unpublished) report survival of transplanted material for periods up to a year.

The seawater in the laboratory studies has included natural bay water as well as synthetic (Instant Ocean) seawater (McMillan, unpublished). The growth of the seagrasses in synthetic seawater suggests that their survival is less dependent upon the source of the medium than upon factors of salinity, temperature and light.

The aeration of the seawater in the culture vessels represents a variable among the studies. Fuss and Kelly (1969) aerated their cultures continuously by using a flowing seawater system. McMahan (1968) aerated his aquaria for short intervals during the day and McMillan (unpublished) has cultured five seagrass species without aeration. In the latter technique, however, McMillan used 5-liter glass jars, the smallest of those in the comparison of Table 5. The depth of the water in the Fuss and Kelly (1969) cultures was 40 cm above the substrate and in the McMillan (unpublished) cultures only 13 cm.

A comparison of substrates was included in the McMahan (1968) and McMillan (unpublished) studies. McMahan reported that there was no apparent difference in plant roots or leaves of *Halodule* growing in the gravel bottom or natural bay sediment. McMillan transplanted five seagrasses into two soils obtained 200 miles inland from the Gulf of Mexico. The river sand and fine sandy loam of central Texas were both highly calcareous, however. After five months, *Halophila*, *Thalassia* and *Ruppia* showed greater

survival in the loam. *Ruppia* survived in both soils for five months but flowered only in the loam. *Syringodium* survived for five months in both soils equally well, but *Halodule* had poor survival in either test condition.

A broad tolerance of seagrasses to light intensity is indicated by the various culture techniques (Table 5). Some of the transplanted seagrasses survived equally well under outdoor intensities and in growth chambers with artificial light (1800 ft-c.; McMillan and Moseley, 1967). Other seagrasses have been kept for several months under light intensities of 600-1000 ft-c (McMillan, unpublished). McMahan (1968) reported a light intensity of 300 ft-c in his experimental cultures. The above light intensities are those at the surface of the culture vessels (Table 5). Those at the leaf surfaces were probably different and of lower intensity.

Some of the studies were concerned with keeping the culture vessels free of algae. Fuss and Kelly (1969) tried biological agents to clear the algae selectively. McMillan (unpublished) transplanted seagrasses into clear synthetic seawater and into synthetic seawater with dense algal growth. Survival of the seagrasses did not correlate with the algal-free condition of the aquaria. *Halophila*, for example, was thriving in culture vessels in which the algal growth was so dense that the seagrass could not be observed in 13 cm of water, suggesting a tolerance for very low light intensity as well as algal associates.

McRoy (unpublished) has successfully used a technique of collecting eelgrass *Zostera marina* from its natural habitat with a large plastic coring tube 17 cm in diameter. This core took a root-rhizome and sediment mat about 15 to 20 cm thick and the whole core was immediately transferred to a 3-liter plastic container, used as a marine "flower pot". These were kept in seawater until shipping to Fairbanks by air freight. In Fairbanks the eelgrass pots have been kept in 25 and 50 gal recirculating aquaria with synthetic seawater (Instant Ocean) and under artificial lights. Temperature and light are controlled to approximate natural cycles and the plants have shown good growth since the time of transplanting; the process of flowering and seed production, although already begun at the time of transplanting, was completed.

Table 5. Comparison of techniques for culturing seagrasses.

	McMillan and Moseley (1967)	McMahan (1968)	Marmelstein et al. (1968)	Fuss and Kelly (1969)	Thorhaug (unpubl)	McMillan (unpubl) ²	McRoy (unpubl) ³	Phillips (1972)
Location of Study	Pt. Aransas Texas	Pt. Isabel Texas	Panama City Florida	St. Petersburg Florida	Miami Florida	Austin Texas	Fairbanks Alaska	Puget Sound Washington
Seagrasses Cultured¹	T,S,HI,Hd,R	S,Hd	T	T,Hd	T	T,S,HI,Hd,R	Z	Z
Collection Site	Redfish Bay	Lower Laguna Madre	St. Andrews Bay, Biscayne Bay	Boca Ciega Bay	Not stated	Redfish Bay	Izembek Lagoon, Sawmill Bay, Alaska	Puget Sound
Time of Transplanting	Mid-June	?	?	Late July	?	January, March-April July-August	March, July	May
Duration of Culture Studies (days)	55	42	14-28	up to 365	up to 365	up to 365	~200	29
Type of Study	salinity tolerance	salinity tolerance	photoperiodic response	culture methods	culture methods	salinity tolerance, photoperiodic response, culture methods	culture methods	growth
Type of Container								
a. Outdoor	ovoid concrete tanks, 4m ² area	—	—	wooden tank, 1000 liters	wooden box, expoxy-resin coated, 1728 liters	—	—	—
b. Indoor	wooden box, paraffin coated, 648 liters	13 liter glass jars	75 liter polyethylene cans	plexiglas aquaria, 125 liters	size not indicated	5 liter glass jars	3 liter plastic cups in coated aquaria	glass tubes no size

Table 5. (continued)

	McMillan Moseley (1967)	McMahan (1968)	Marmelstein et al. (1968)	Fuss and Kelly (1969)	Thorhaug (unpubl)	McMillan (unpubl) ²	McRoy (unpubl) ³	Phillips (1972)
Transplanting Substrate								
a. Type	bay sediment	gravel or bay sediment	beach sand	builder's sand over gravel	calcareous beach sand over limestone gravel	calcareous river sand or fine sandy loam	intact natural sediments	water culture no substrate
b. Depth of Substrate	5-7.5 cm (in plastic trays, 30 x 20 x 7.5 cm)	gravel directly into jar (depth not indicated)	7.5-10 cm directly into can	20 cm sand over 40 cm gravel in trays, 100 x 100 x 30 cm (outdoors) 6 cm sand over 3 cm gravel (indoors)	36 cm sand over 10 cm gravel on sheets of 14 gauge aluminum suspended 4 cm above bottom (outdoors)	9.5 cm in 500 ml plastic cups, 3 per jar	15 cm in plastic cups	
Water								
a. Depth Above Substrate	45 cm (outdoors) ? 30 cm (indoor)		50 cm	40 cm	70 cm	13 cm	15 cm	—
b. Water Exchange	tap water added	seawater changed every 7 days	8 liter changed every 7 days	flowing seawater (140 liter per hr)	flowing seawater	tap water added	—	enriched seawater changed weekly
c. CO₂ added	—	70-95 ppm per 24 hr	—	—	—	—	—	—
d. Aeration	—	1/4 hr per 24 hr	—	recirculated (aquaria)	recirculated (aquaria)	—	recirculated	—

Table 5. (continued)

	McMillan Moseley (1967)	McMahan (1968)	Marmelstein et al. (1968)	Fuss and Kelly (1969)	Thorhaug (unpubl)	McMillan (unpubl) ²	McRoy (unpubl) ³	Phillips (1972)
e. Temp. (°C)	not controlled (outdoors) 22 (indoor)	25	27-30 (outdoors)	not controlled 25 (indoor)	16-32	20-30	10-15	controlled but not stated
f. Salinity (‰)	28-31 and increasing hypersalinity to 70-75	3.5-87.5	28-34	32-36	22-38	37 and 0-95 seawater (Instant Ocean)	~33 synthetic seawater (Instant Ocean)	not stated

1. Seagrasses are abbreviated: T, *Thalassia testudinum* König and Sims; S, *Syringodium filiforme* Jutzing; Hl, *Halophila engelmanni* Aschers.; Hd, *Halodule beaudetti* den Hartog (*Diplanthera wrightii* (Aschers) Aschers.; R, *Ruppia maritima* L.; Z, *Zostera marina* L.

2. Austin, Texas is located 200 miles from the Gulf Coast. Plants were transplanted to a greenhouse at the University of Texas.

3. Fairbanks, Alaska is located 500 miles from the coast.

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