C00-3054-4

NOTICE

This report was prepared as an account of work sponsored by the United States Government. Neither the United States nor the United States Atomic Energy Commission, nor any of their employees, nor any of their contractors, subcontractors, or their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness or usefulness of any information, apparatus, product or process disclosed, or represents that its use would not infringe privately owned rights.

Educing the functional relationships among the diatom assemblages within sublittoral salt marsh epiphytic communities.*

CONF-720623--1

J J LEE, M E McENERY, E M KENNEDY & H RUBIN

City College of the City University of New York, Convent Avenue at 138th Street, New York, New York 10031, USA

SUMMARY

MASTER

In salt marsh epiphytic communities species diversity is high among the bacterial, diatom, protozoan, and micrometazoan assemblages. Carbon fixation by Enteromorpha, the dominant macrophyte in the community, gradually increases during May and reaches a peak ($140 \mu\text{Mmg}^{-1}\text{hr}^{-1}$) in early July before declining in August. Carbon fixation by the epiphytic assemblage on Enteromorpha is greater ($200 \mu\text{Mmg}^{-1}\text{hr}^{-1}$) at the peak of fixation in late July. In short term field experiments both the algal and bacterial assemblages actively utilized labeled low molecular weight organic compounds. In the marshes tested more urea, mannitol, and a selected amino acid mixture ($\sim 100 \mu\text{Mmg}^{-1}\text{hr}^{-1}$) was taken up week by week over the summer by the algae than by the bacteria ($\sim 10 \mu\text{Mg}^{-1}\text{hr}^{-1}$). Nutritional studies of selected species of algae led to the design of a series of differential media which were used to gain insight into the auxotrophic profile of the community throughout the growing season. In addition to the recognition of bacterial colonies were were able to construct a dichotomous diagnostic key for the recognition of various diatom colonies. Diatom community structure and succession was also studied by light microscopy and correlated with the above. The data from our studies suggests that the dissolved organic nutrients which arise from the degradation of marsh grasses play a central role in the nutrition, community regulation, and succession within the algal assemblage of the community.

* Supported by US AEC (C00 3254-4)

DISTRIBUTION OF THIS DOCUMENT IS UNLIMITED

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency Thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

INTRODUCTION

Burgeoning human populations and acceleration of man's activities are causing increasing complexities and stresses in many environments. Never has there been greater need for understanding those structure-function relationships in natural ecosystems which could be used to help establish realistic guidelines for more effective use and management of natural resources. Although the pioneering work of Winogradsky and Beijerinck long ago showed that microbial assemblages of unstressed natural communities tend to be extremely complex and responsive to changes in environmental conditions, even now the task of identifying and understanding their intricacies seems formidable. Not without justification, most approaches to assessment of natural microbial activity have tended to be either quantitative overviews or taxonomically oriented distribution and seasonal succession studies with details of associated macroenvironmental conditions for a limited area over a narrow time span (Aleen 1950, Brock 1971, Castenholz 1961, 1963, Hendey 1964, Hopkins 1964a and b, Patrick 1967, 1968, Round 1971, Saunders 1957). Most laboratory studies to date involve relatively simple, stable conditions without interspecific competition, succession, accessory organic, or other features of more complex natural habitats, or were agnotobiotic (Beyers 1963, McIntire and Wulff 1969, Phinney and McIntire 1963).

Our special interest over the past decade has been the characterization of the microbial and micrometazoan populations of salt marsh epiphytic and epibenthic communities in comparable unpolluted and polluted areas. Although there is a great deal of knowledge on salt marshes and shoal water marine habitats (Teal and Kanwisher 1966, 1970, Pomeroy 1959, 1963, 1970, Jeffries 1962, Jitts 1959, Odum and Smalley 1959, Pomeroy *et al.* 1972, Teal 1962, Stowe *et al.* 1971, Burkholder 1956, Burkholder and Burkholder 1957, Udel *et al.* 1969) very little is known of the microbial and micrometazoan assemblages which are so important in the nutritional transformations underlying the marine detritus food web. The diversity of forms within the aufwuchs community is large but manipulatable for modeling in the laboratory. Within 1 cm³ live perhaps 10⁶ organisms belonging to several hundred species (Table 1). What are the bases which

underly the huge diversity of species on the same trophic level? If we understand this we would know much about the subtle variables which regulate population structure, succession, and information within the community.

MATERIALS AND METHODS

Most of the samples collected and the field observations were made at Towd Point, North Sea Harbor, Southampton, Long Island, New York, USA (N 40°55' W 72°25'; Lee et al. 1966, 1970). For comparative purposes in 1971 there were some experiments and collections at Sippewisset Marsh in Falmouth, near Woods Hole, Massachusetts, USA (N 41°32' W 70°40').

Measurements of primary productivity and respiration were made at Towd Point using Gilson #5 all glass differential manometers mounted on a float. The manometers were secured to the float by means of a stainless steel holder and channel bracket (Gilson Medical Electronics, 300 West Beltline Highway, Middleton, Wisconsin 53562). Six manometer systems were mounted on each float so that the reaction flasks float 11.5-12.5 cm below the surface. Three flasks on each were used as light bottles and three were completely wrapped in heavy duty aluminium foil to serve as dark bottles. In both light and dark sides of the float one flask was inoculated with either: 1) carefully washed Enteromorpha intestinalis; 2) the epiphytic community from above; or 3) the mixed community. A piece of filter paper saturated with 20% KOH was placed in the center well of the dark bottles. Approximately 50-100 mg (dry weight) of the sample was placed in each reaction vessel with 2.5 ml water from the collecting site and 0.4 mM NaHCO₃. At the conclusion of the experiments the samples were harvested by filtration onto previously weighed Millipore HA filter discs and dried to a constant weight in a vacuum oven.

Experiments were performed in duplicate under a variety of

climatic conditions twice a week for 2 summers. The data presented are for the summer of 1969. The data was fitted to the curves presented by means of a curve fitting program written in Fortran IV for an IBM 360/50. Conversion of the data from O_2 net production to g C followed the suggestions of Wetlake (1969). An ISCO spectroradiometer was used to measure spectral intensity. The effect of temperature and illumination was evaluated separately in the laboratory. A Gilson (Model GRP 20) illuminated refrigerated respirometer was used with 5 axenic fully-differentiated Enteromorpha as inocula. India ink was added to the water bath as a neutral density filter.

Once a week throughout the summer of 1971 in the marshes at Towd Point and Sippewisset small samples of the epiphytic community from a particular quadrant in each marsh were incubated in sterile sea water from the station enriched with either ^{14}C labeled ($1 \mu Ci/\mu M$) glycerol, urea, glucose, mannitol, or a mixture of the following amino acids: glycine, glutamic acid, alanine, and aspartic acid. Labeled $NaH^{14}CO_3$ served as control. After 2 hrs incubation in the light and under water at ambient field conditions the community was vigorously agitated and then harvested by filtration through a preweighed Millipore SS ($3 \mu m$) filter. The SS filter was selected to retain the algae and allow the bacteria to pass through. After the filter was rinsed with "cold" (unlabeled), previously Millipore filtered seawater, the filtrate was refiltered by the second filter. The filters were slowly dried to a constant weight in a vacuum oven. No attempt was made to capture and measure the $^{14}CO_2$ given off during the incubation period.

Once a week during the summer of 1970 for 12 weeks beginning with 10 June small samples (0.2 g dry weight) of Enteromorpha were aseptically removed from the environment and inoculated into screw-cap test tubes (25 mm x 150 mm) containing 30 ml of sterile sea water from the same environment. At a nearby field laboratory the sample

was agitated vigorously with a Vortex mixer and aseptically inoculated into a series of differential media designed to give insight into the nutritional requirements of various members of the community (Lee, McEnery, Kennedy and Rubin, ms in preparation). The remainder of the sample was examined by phase microscopy and then fixed in alcohol. Permanent microscope slides of each of the samples were also prepared. In each week's sample, at least 1,000 clearly identifiable diatoms in 50 or more randomly selected fields were enumerated. After incubation at 25 C in an illuminated (18 hr light/6 hr dark) Sherer Cel 4-4 environmental chamber the plates were examined for both bacterial and diatom colonies. Previous experience with diatoms suggested to us that it might be possible to differentiate diatoms on the basis of colonial morphology. After preliminary examination of the diatom colonies on the differential media we constructed a dichotomous diagnostic key which was used in the identification of the various colonial types. Under a dissecting microscope a thin spatula was used to pick colonies. The colonies were then placed in 50% alcohol in the depressions of 9-hole spot plates. After washing in distilled water the colonies were dehydrated through a graded series of alcohols and mounted in Zeiss phase contrast mounting medium. Photomicrographs were taken through the trinocular tube of a Wild M-5 stereomicroscope. All were taken on Kodak Panatomic X Film developed with Kodak D-76 diluted 1:1.

RESULTS

At North Sea Harbor the macrophytic standing crop is seasonal. From late May to early August Enteromorpha intestinalis is the dominant macrophyte. Carbon fixation by Enteromorpha gradually increases during May and reaches a peak ($140 \mu\text{M mg}^{-1} \text{hr}^{-1}$; $y = 0.56 + 0.812x - 0.0483x^2$) in early July before declining in August. The epiphytes from Enteromorpha, when incubated by themselves, fixed more carbon than did Enteromorpha alone for most of the summer reaching a

peak ($200 \mu\text{M mg}^{-1}\text{hr}^{-1}$; $y = -3.12 + 1.564x - 0.0820x^2$) in late July. The undisturbed macrophyte and its epiphytes was about as productive ($130 \mu\text{M mg}^{-1}\text{hr}^{-1}$; $y = 0.28 + 0.597x - 0.037x^2$) as Enteromorpha by itself (Fig. 1). Respiration of the mixed community increased gradually during the summer reaching $\sim 60 \mu\text{M CO}_2\text{mg}^{-1}\text{hr}^{-1}$; ($y = -0.093 + 0.294x - 0.0145x^2$) in the latter part of the summer.

In the laboratory photosynthesis at 25 C was directly proportional to spectral intensity over the range tested ($15 \mu\text{W/cm}^2$ - $318 \mu\text{W/cm}^2$). Within the temperature range observed in the field during most of the summer, 20-28 C, the photosynthetic rate of axenic Enteromorpha was quite high ($> 1.5 \text{ ml O}_2 \text{ mg}^{-1}\text{hr}^{-1}$) with a maximum at 24 C.

At Sippewisset Marsh more urea, glycerol, glucose and the amino acid mixture was taken up week by week over the summer by the algal compartment ($> 3 \mu\text{M}$) ($\sim 100 \mu\text{M mg}^{-1}\text{hr}^{-1}$) than was taken up by the bacteria ($\sim 10 \mu\text{M mg}^{-1}\text{hr}^{-1}$) (Figs. 3 A-F). At Towd Point the trend was similar although at times during the summer there was no significant difference in the uptake by either fraction of the community. Uptake of $\text{NaH}^{14}\text{CO}_4$, a measure of photosynthesis, was generally an order of magnitude greater than any of the organic substrates. In both marshes considerable fluctuation in substrate utilization was observed over the summer. At Southampton glycerol utilization gradually increased over the summer while this trend was not observed at Sippewisset. In both marshes urea utilization by the bacteria ($< 3 > 0.45 \mu\text{M}$ fraction) rose by more than an order of magnitude during the early summer and gradually diminished toward the end.

Similar fluctuations in nutritional requirements were evidenced by the growth of bacteria and algae on the various differential media. A total of 65 types of diatom colonies were recognized on the differential media. Representative colonial types are illustrated (Figs. 4 A-I). Almost one half of the colonial types (32) grew at different times on unenriched sea water from the same field station. The addition of KNO_3 (0.01%) and $\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$ (0.01%) to natural sea

water reduced the total numbers of colonies and halved the number of species isolated. Even fewer colonies developed on erdschreiber. Synthetic erdschreiber, medium C3, was one of the best media tested (Fig. 5A); 42 different types and > 600 colonies grew on it during the course of the summer. Comparable numbers of colonial types and total numbers of colonies grew on medium D7 (enriched with autoclaved Enteromorpha extract) (Fig. 5B). The pattern of organisms which grew on the media over the summer was different.

Both media were among the more selective for colony types. Ophephora martyi, Achnanthes hauckiana varieties, Synedra and Achnanthes spp and Navicula spp were common to both media. Fragilaria construens, Nitzschia spp and Melosira nummuloides were also isolated on medium C₃. On medium D₇ Nitzschia sp ("F", a new species) colonies were also found. A more detailed analysis of these experiments is being prepared for a longer paper (Lee, McEnery, Kennedy and Rubin ms).

The fluctuations in diatom colony growth on various differential media closely follow changes in the community structure. Nine species, Achnanthes hauckiana sensu stricto and (var. CD), Cocconeis scutellum, Achnanthes sp ("J"), Achnanthes sp ("M"), Cocconeis placentula, Fragilaria construens, Amphora acutiuscula, Synedra affinis, and Navicula sp ("BELS"), dominated the Enteromorpha epiphytic community structure (~ 64% total) during the summer months (Fig. 2). A total of 218 species were recognized; Navicula and Achnanthes were represented by the most species. Two computer programs were written to: a) correlate the abundance of pairs of species over time and b) correlate the appearance-time of pairs of species in the community. Some of the highest abundance correlation coefficients were found between Achnanthes hauckiana (var. AB)-Nitzschia panduriformis (0.900); A. hauckiana (var. AB)-Navicula halophila (0.934); A. hauckiana (var. AB)- Nitzschia acicularis (0.92); Nitzschia panduriformis-N. acicularis (0.963); N. panduriformis-N. closterium (0.991); N. panduriformis-N. sigmaformis (0.994); Nitzschia sigma-Navicula digito-radiata (0.914). Some negative correlations, i.e., Achnanthes wellsiae-

8.

Synedra affinis (-0.622); A. wellsiae-Melosira nummuloides (-0.606) and Achnanthes sp ("M") and M. nummuloides (-0.622) were also noted. Positive appearance time correlations were noted between N. panduriformis-N. acicularis-N. closterium-N. sigmaformis (1.00) and among other species. Most negatively correlated were Amphora acutiuscula-Navicula digito-radiata (-0.714); A. acutiuscula-A. hauckiana (-0.714); A. hauckiana (var. CD)-Synedra gallionii (0.683) and Navicula sp (BELS") and N. digito-radiata (-0.714).

DISCUSSION

Enteromorpha and its epiphytic community is very productive at our field station in Southampton. We estimate an annual net production by Enteromorpha and its aufwuchs to be $\sim 0.5-1 \text{ KgC/m}^2/\text{yr}$ or $\sim 440 \text{ KgC/yr}$ in Towd Point embayment. On an annual m^2 basis the primary production by the Enteromorpha community is $1/2-2/3$ x that of the Thalassia testudinum community studied by Jones (1968); $10 \times$ that of the Zostera marina community studied by Marshal (1969); $\sim 2/3$ the stream inside production by the Spartina alterniflora community measured by Stowe et al. (1971) and comparable to that found by Pomeroy (1959) in his studies of algal productivity in Georgia salt marshes.

Though the concept of heterotrophy in littoral and sublittoral benthic algae is well established (Lewin and Guillard 1963, Lewin 1963, Lewin and Lewin 1967, Lewin and Hellebust 1970, Round 1971) as is the measurement of net substrate uptake to give estimates of relative heterotrophic potentials (Parsons and Strickland 1961, Vaccaro et al. 1968, Vaccaro and Jannasch 1966, 1967, Hobbie and Wright 1965, Hellebust and Guillard 1969). The task of detailing the subtle niche relationships between the huge variety of species which actually exploit any particular environmental situation has not really even been started. With the development of our new media for the isolation and culture of most of the microflora from the community we now have the tools to dissect, study, and model the ecologically meaningful biotic relationships among community members in small laboratory microcosms. Thus far we have selected 12

species of algae, from among the ~ 400 clones we have in axenic culture, for detailed study. We have completed studies on: their heterotrophic requirements and have begun some paired synergistic and antagonistic experiments (Stone, dissertation in progress); the effects of light quality (Saks and Lee 1971), acute ionizing radiation (both UV and γ), and acute and chronic thermal stress on their growth and survival (Saks and Lee 1972); their abundance and distribution in the natural community and on some interrelationships between the algae, bacteria and protozoan and micrometazoan herbivores (Lee *et al.* 1966, 1970, 1971, Muller and Lee, 1969, Tietjen *et al.* 1970). At present we have only clues to the complexities of one salt marsh epiphytic community. Will we really ever understand the biology of 1 cm³ of a natural community? We hope so.

LITERATURE CITED

- ALEEM A A. 1950. Distribution and ecology of British marine littoral diatoms. - J. Ecol. 38:75-106.
- ALLEN K R. 1971. Relation between production and biomass. - J. Fish. Res. Bd. Canada 28:1573-1581.
- BEYERS R J. 1963. The metabolism of twelve aquatic laboratory microecosystems. - Ecol. Monogr. 33:281-306.
- BROCK T D. 1971. Microbial growth rates in nature. - Bact. Rev. 35:39-58.
- BURKHOLDER P R. 1956. Studies on the nutritive value of Spartina grass growing in the marsh areas of coastal Georgia. - Bull. Torrey Bot. Club 83:327-334.
- BURKHOLDER P R & BORNSIDE G H. 1957. Decomposition of marsh grass by aerobic marine bacteria. - Bull. Torrey Bot. Club 84:366-383.
- CASTENHOLZ R W. 1961. The effect of grazing on marine littoral diatom populations. - Ecol. 42:783-794.
- CASTENHOLZ R W. 1963. An experimental study of the vertical distribution of littoral marine diatoms. - Limnol. Oceanogr. 8:450-463.
- CASTENHOLZ R W. 1964. The effect of daylength and light intensity on the growth of littoral marine diatoms in culture. - Physiol. Plantarum 17:951-963.

- GRØNTVED J. 1960. On the productivity of the microbenthos and phytoplankton in some Danish fjords. - Medd. Komm. Danm. Fiskeri-og. Havunders., N. S. 3:55-62.
- GRØNTVED J. 1962. Preliminary report of the productivity of microbenthos and phytoplankton of the Danish Waddensea. - Medd. Komm. Danm. Fiskeri-og. Havunders., N. S. 3:347-378.
- HENDEY N I. 1964. An introductory account of the smaller algae of British coastal waters. Part V. Bacillariophyceae (Diatoms) - Min. Agr. Fisheries & Food. Fisheries Invest. Series IV.
- HOBBIE J E & WRIGHT R T. 1965. Bioassay with bacterial uptake kinetics: glucose in freshwater. - Limnol. Oceanogr. 10:471-474.
- HOLM-HANSEN Ø. 1969. Determination of microbial biomass in ocean profiles. - Limnol. Oceanogr. 14:740-747.
- JANNASH H W. 1968. Growth characteristics of heterotrophic bacteria in seawater. - J. Bacterial. (in press).
- JEFFRIES H P. 1962. The atypical phosphate cycle of estuaries in relation to benthic metabolism. Symposium on the Environmental Chemistry of Marine Sediments. Univ. Rhode Island Grad. School Oceanogr. Occ. Pap. No. 1:58-68.
- JITTS H R. 1959. The absorption of phosphate by estuarine bottom deposits. - Australian J. Mar. Freshw. Res. 10:7-21.
- JONES J A. 1968. Primary productivity of the tropical marine turtle grass, Thalassia testudinum Konig, and its epiphytes. - Univ. Miami, unpublished PhD thesis.
- LEE J J, McENERY M, PIERCE S, FREUDENTHAL H D, & MULLER W. 1966. Tracer experiments in feeding littoral foraminifera. - J. Protozool. 13:659-670.
- LEE J J, McENERY M, KENNEDY E, & RUBIN H. 1972. A nutritional analysis of a sublittoral epiphytic diatom assemblage from a Long Island salt marsh - in press.
- LEE J J, TIETJEN J H, STONE R J, MULLER W A, RULLMAN J, & McENERY M. 1970. The cultivation and physiological ecology of members of salt marsh epiphytic communities. - Helgolander wiss. Meeres., 20:136-156.
- LEE J J, TIETJEN J H, STONE R J, MULLER W A, McENERY M, SAKS N M, MASTROPAOLO & KENNEDY E. 1971. The effect of environmental stress on the community structure, productivity, energy flow and mineral cycling in salt marsh epiphytic communities. - Third Nat. Sympos. Radioecol., in press.

- LEWIN J C. 1963. Heterotrophy in marine diatoms. -In: Marine Microbiology, ed C H Oppenheimer, Charles C. Thomas Publ. pp 229-235.
- LEWIN J & GUILLARD R R L. 1963. Diatoms. - Ann. Rev. Micro. 17:373-414.
- LEWIN J & HELLEBUST J A. 1970. Heterotrophic nutrition of the marine pennate diatom, Cylindrotheca fusiformis. - Can. J. Microbiol. 16:1123-1129.
- LEWIN J & LEWIN R A. 1960. Autotrophy and heterotrophy in marine littoral diatoms. - Can. J. Microbiol. 6:127-134.
- MARSHALL N. 1969. Trophic relationships in shoal benthic environments. -In: Marine food chains, ed J H Steele, Oliver & Boyd, Edinburgh:52-66.
- McINTIRE C D & WULFF B L. 1969. A laboratory method for the study of marine benthic diatoms. - Limnol. Oceanogr. 14:667-678.
- McINTOSH R P. 1967. An index of diversity and the relation of certain concepts to diversity. - Ecol. 48:392-404.
- MULLER W A & LEE J J. 1969. Apparent indispensability of bacteria in foraminiferan nutrition. - J. Protozool. 16:471-478.
- ODUM E P & SMALLEY E. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. Proc. Natl. Acad. Sci. 45:617-622.
- PARSONS T R & STRICKLAND J D H. 1961. On the production of particulate organic carbon by heterotrophic processes in seawater. - Deep-Sea Res. 8:211-222.
- PATRICK R. 1963. The structure of diatom communities under varying ecological conditions. - Ann. NY Acad. Sci. 108:353-358.
- PATRICK R. 1964. A discussion of natural and abnormal diatom communities. -In: Algae and man, ed. D F Jackson, Plenum Press, New York:185-204.
- PATRICK R. 1967. Diatom communities in estuaries. -In: Estuaries, ed. G. Luaff, Amer. Assn. Advance. Sci., Washington.
- PATRICK R. 1968. The structure of diatom communities in similar ecological conditions. - Amer. Natur. 102:173-183.
- PHINNEY H K & McINTIRE C D. 1965. Effect of temperature on metabolism of periphyton communities, developed in laboratory streams. - Limnol. Oceanogr. 10:341-344.
- POMEROY L R. 1959. Algal productivity in salt marshes of Georgia. - Limnol. Oceanogr. 4:386-397.

- POMEROY L R. 1963. Experimental studies of the turnover of phosphate in marine environments. - In: Radioecology, ed. V. Schultz & A W Klements, Reinhold, New York:163-166.
- POMEROY L R, SHENTON L R, JONES R D H & REIMOLD. 1972. Nutrient flux in estuaries. - In: Nutrients and eutrophication, ed. G. E. Kines & J. E. Hobbie. ASLO Special Publ., Lawrence, Kans.
- ROUND F E. 1971. Benthic marine diatoms. - Oceanogr. Mar. Biol. Ann. Rev. 9:83-139.
- SAKS N M & LEE J J. 1972. Radiosensitivity and light quality responses of salt marsh epiphytic algae. Nat. Symp. Radioecol. III, Proc. (in press).
- SAKS N M & LEE J J. 1972. The differential sensitivity of various species of salt marsh epiphytic algae to ionizing radiation and thermal stress. -Sympos. on Interaction of Radioactive Contaminants with the Constituents of the Marine Environment. Proc., in press.
- SAUNDERS G W. 1957. Interrelation of dissolved organic matter and phytoplankton. - Bot. Rev. 23:389-410.
- SLOAN P R & STRICKLAND J D H. 1966. Heterotrophy of four marine phytoplankters at low substrate concentrations. -J. Phycol. 2:29-32.
- STOWE W C, KIRBY C, BERKICH S & GOSSELINK J G. 1971. Primary production in a small saline lake in Barataria Bay Louisiana. -Coastal Studies Bull. #6: Special Sea Grant Issue, February.
- TEAL J M. 1962. Energy flow in the salt marsh ecosystem of Georgia. -Ecol. 43:614-624.
- TEAL J M & KANWISHER J. 1966. Gas transport in the marsh grass, Spartina alterniflora. - J. Exp. Bot. 17:355-361.
- TEAL J M & KANWISHER J W. 1970. Total energy balance in salt marsh grasses. - Ecol. 51:690-695.
- TIETJEN J H, LEE J J, RULLMAN J, GREENGART A. & TROMPETER J. 1970. Gnotobiotic culture and physiological ecology of the marine nematode, Rhabditis marina Bastian. Limnol. Oceanogr. 15:535-543.
- UDELL H F, ZARUDSKY J & DOHENY T E. 1969. Productivity and nutrient values of plants growing in the salt marshes of the town of Hempstead, Long Island. - Bull. Torrey Bot. Club 96(1):42-51.
- VACCARO R F, HICKS S E, JANNASCH H W & CAREY F G. 1968. The occurrence and role of glucose in sea water. - Limnol. Oceanogr. 13:356-360.

VACCARO RF & JANNASCH H W. 1966. Studies on heterotrophic activity in seawater based on glucose in seawater. - Limnol. Oceanogr. 11:596-607.

VACCARO R F & JANNASCH H W. 1967. Variations in uptake kinetics for glucose by natural populations in seawater. - Limnol. Oceanogr. 12:540-542.

WESTLAKE D F. 1969. Units and comparability, pp. 113-117. In: A Manual on methods for measuring primary production in aquatic environments, ed. R A Vollenweide, I B P Handbook 12, F A David, Inc. Philadelphia, Pa.

TABLE 1

Number of organisms found in an idealized cm^3 sample of a community epiphytic on Enteromorpha in an unpolluted salt marsh.

<u>Organisms</u>	<u>Concentration</u>	<u>#species in one sample</u>	<u>Total # species in marsh</u>
Diatoms	$1 \times 10^3 - 10^4$	75-100	~250
Chlorophytes	$10 - 10^3$	5-10	>30
Enteromorpha zoospores	1×10^3	varies	
Dinoflagellates	10-100	2	~ 30
Prasinophytes	1-2	>1	
Euglenophytes	$10 - 10^2$	varies	~ 6
Blue greens	$10 - 10^3$	2	
Yeasts	5-10	>1	> 10
Bacteria	$\sim 10^4$	~20	~ 75
Zooflagellates, colorless dinoflagellates, Euglenoids	$10 - 10^2$	~ 4	> 50
Amoeba	$\sim 10 - 10^2$	2	> 12
Heliozoa	rare	1-2	1
Foraminifera	$10 - 10^3$	2-15	> 40
Ciliates	$10 - 10^2$	4-8	> 50
Gastrotrichs	2-10	1	
Rotifers	$10 - 10^2$	2	
Nematodes	$10^2 - 10^3$	3-5	> 40
Microcrustacea	$10 - 10^2$	varies	
Gastropods	~ 10.	1	
Other Micrometazoa	< 10	1	

Figure 1

Figure 2

..... Sea water
 - - - - - Erdschreiber
 - - - - - A1
 _____ Total for all media

NUMBER OF COLONIES / C

10^7
 10^6
 10^5
 10^4

1 2 3 4 5 6 7 8 9 10 11 12

WEEK

Figure 3

MOLES / GRAM / HOUR

LEGEND
SS Filters: — Southampton, Woods Hole
HA Filters: --- Southampton, - - - Woods Hole

FIGURE 4

FIGURE 5