ECOLOGY OF A NEW ENGLAND SALT MARSH[1]

Scott W. Nixon and Candace A. Oviatt

Graduate School of Oceanography
University of Rhode Island, Kingston, Rhode Island 02881

TABLE OF CONTENTS

ABSTRACT

Measurements of the abundance of major populations, their metabolism, and the seasonal patterns of total system metabolism throughout a year were used to develop energy-flow diagrams for a New England salt-marsh embayment. The annual ecological energy budget for the embayment indicates that consumption exceeds production, so that the system must depend on inputs of organic detritus from marsh grasses. Gross production ranged from almost zero in winter to about 5 g O_2 m^{-2} day^{-1} in summer. Respiration values were similar, but slightly higher, with the maximum difference observed in fall. Populations of shrimp and fish were largest in fall, with a much smaller peak in spring. Few animals were present in the embayment from May to July, but fall populations of shrimp ranged from 250 to 800 m^{-2} and fish averaged over 10 m^{-2}. Birds were most abundant in winter and spring. In spite of high numbers, no evidence was found that the marsh embayment exported large amounts of shrimp or fish to the estuary. Production of aboveground emergent grasses on the marsh equaled 840 g m^{-2} for tall *Spartina alterniflora*, 432 g m^{-2} for short *S. alterniflora*, and 430 g m^{-2} for *S. patens*. These values are similar to those for New York marshes, but substantially lower than the southern marsh types. The efficiency of production of marsh grasses in the New England marsh was lower than reported for southern areas.

A simulation model based on the laboratory and field metabolism and biomass measurements of parts of the embayment system was developed to predict diurnal patterns of dissolved oxygen in the marsh. The model was verified with field measurements of diurnal oxygen curves. The model indicated the importance of the timing of high tides in determining oxygen levels and was used to explore simulated additions of sewage BOD and increases in temperature.

Key words: *New England, salt marsh, ecosystem, embayment, oxygen, model, Spartina, Palaemonetes, Fundulus, detritus, production, energy*

INTRODUCTION

The extensive salt marshes of the Atlantic and Gulf coasts of the United States are among the most frequently studied ecological systems. Although marshes are present all along the coast, those in New England tend to be small and characterized by a heavy peat substrate, whereas the marshes south of New Jersey are better developed, with mineral sediments typical of a nonglaciated coastal plain (Chapman 1940, 1960). Most of our knowledge of the marsh ecosystem has come from studies of the latter type of salt marsh. The well-known synthetic treatment of many studies in the marshes of Sapelo Island, Georgia, by Teal (1962) has served for 10 years as a summary statement of ecological energy flow in this type of system. Drawing primarily on earlier work by Pomeroy (1959) on sediment algal production, Smalley (1960) on *Spartina* and insect populations, Kuenzler (1961) on mussels, his own work on crabs (Teal 1958, 1959), and his studies with Kanwisher (Teal and Kanwisher 1961) and Duff (Duff and Teal 1965) on gas exchange in marsh grasses and muds, Teal was able to illustrate the great productivity of the emergent grasses and the importance of detritus food chains on the marsh, in contrast to the grazing food chains of terrestrial grasslands.

Few, if any, such studies of ecological energetics have become available for the northern marsh types of New England (Cooper 1969). With the exception of primary productivity measurements on the marshes of Long Island by Udell et al. (1969) and estimates of primary production of sediment algae by Lytle (1969) in Rhode Island, almost all of the work in this region has been devoted to autecological studies of various component species of different marshes (Blum 1968) or to careful determinations of floristic composition, succession, and zonation (Chapman 1940, Miller and Egler 1950, Niering 1961). Because of clear zonation patterns in the northern marshes, the successional vegetation diagram of Miller and Egler may be cited as a structural analog of Teal's diagram of system function. Redfield (1972) has recently given a detailed description of the historical development of New England marshes.

In our efforts to describe the ecological energetics of a New England salt marsh, it also became apparent that little attention has been given anywhere along the coast to the associated networks of shallow tidal embayments and creeks that couple the emergent marsh with the larger estuary. When data are available, they are usually confined to individual species in separate marsh areas, such as studies by Wood (1967) on the physiology of grass shrimp, *Palaemonetes*, and by Schmelz (1964) on the com-
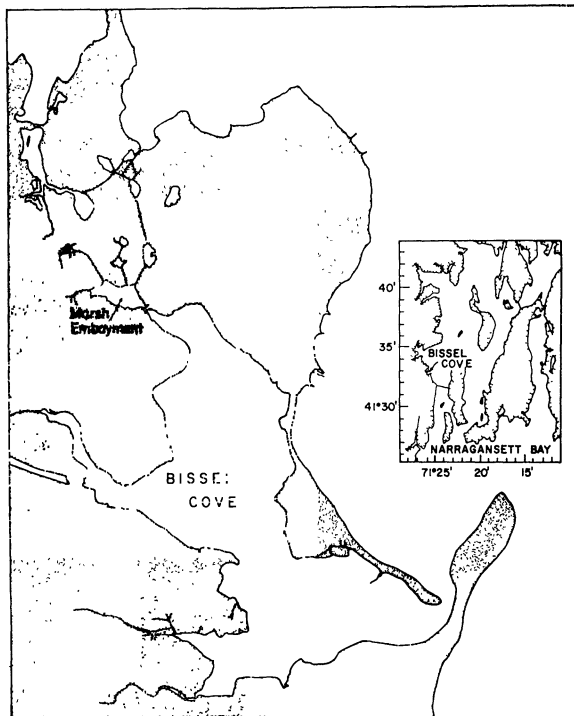
FIG. 1. Location of the marsh study area in Bissel Cove, Narragansett Bay, Rhode Island.

mon mummichog, *Fundulus heteroclitus*. Although some attention has been given to phytoplankton dynamics in the marsh creeks of Georgia (Ragotzkie and Pomeroy 1957, Ragotzkie 1959) and Long Island (Udell et al. 1969), few quantitative data are available on the overall patterns and magnitudes of metabolism of these systems or on the seasonal changes in the size and composition of their major populations. While it is understandable that the conspicuous stands of grass first captured the attention of coastal ecologists, it would seem equally important to understand the dynamics of this interface region of tidal creeks and embayments and to include them in an analysis of the marsh system.

Bissel Cove

Like a miniature of the well-known Barnstable Harbor on Cape Cod, Bissel Cove, the area chosen for this study, shows many of the "family" characteristics of New England marsh areas described by Ayers (1959). The cove and its associated marshes have developed from a coastal indentation that has been partially cut off from the West Passage of Narragansett Bay, R.I., by a barrier bar (Fig. 1). Freshwater inputs to the area from stream drainage and rainfall are small compared with tidal influences, so that the waters are characteristically marine, though great short-term variations in salinity occur. In the northern end of the cove the charac-
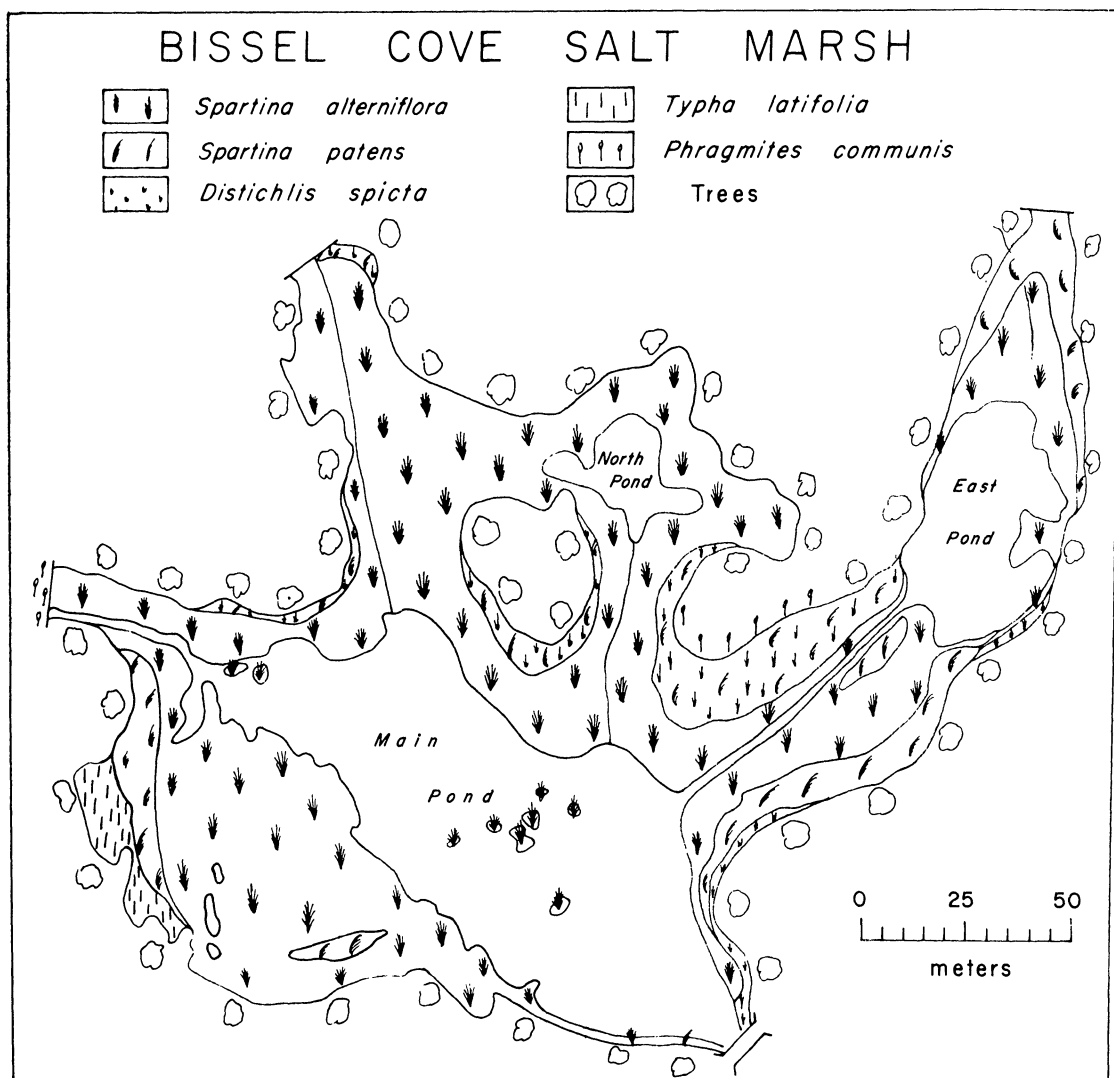
FIG. 2. Vegetation map of the Bissel Cove marsh. The bridge over the embayment mouth is shown at the lower right.

teristic development of marsh and tidal creek networks has been modified somewhat by construction of a bridge over the main creek opening into the cove. As a result, the area beyond the bridge and its underlying culvert is a tidal embayment of 6,600 m² with a mean depth at low tide of about 0.25 m. Small ditches and creeks connect this embayment with a smaller saltwater pond to the east and two still smaller ponds in the north. These satellite ponds have areas of 1,600 m², 500 m², and 450 m² with average depths of about 0.15 m. An examination of old coast and geodetic survey maps indicates that the basic pattern of tidal ponds, emergent grasses, and bordering fringes of white oak shown in Fig. 2 has remained relatively unchanged for at least a hundred years.

The total area of the emergent marsh between the embayment and the trees is 16,800 m². This relatively small size of the combined embayment and emergent grass system, 23,400 m², made it possible to include many parameters in an almost synoptic sampling program and still maintain replication. The presence of a bridge and culvert across the mouth of the embayment instead of a large exposed tidal front provided an opportunity to regulate the tidal activity of the marsh and to get accurate estimates of the total input and output of organisms and detritus from the marsh. Morphological stability, floristic composition, small size, and susceptibility to experimental manipulation made Bissel Cove attractive for study as a model for energy flow in the New England marshes.

METHODS

Production and metabolism measurements

Marsh grass production.—Low altitude aerial photographs taken at 400–1,500 ft were combined with field transect measurements to prepare a vegetation map of the Bissel Cove marsh. A polar planimeter was used to determine the area of coverage of each vegetation type. Production estimates for each grass were taken from replicate one-quarter-square-meter clip quadrats selected by random toss and harvested at the end of the growing season. The collected grasses were then ovendried at 105° C and weighed. In New England marshes with a distinct growing period, each year's crop is easily recognized from another, and the maximum standing crop in the fall can provide an estimate of annual net production, especially where grazing of live grass is minor. In a careful study of North Carolina marshes, Williams and Murdoch (1969) compared estimates obtained in this way with production figures corrected for loss of blades through the growing season. Their results indicate that actual annual net production may be about 15% higher than harvest techniques indicate. No attempt was made to measure the production of new rhizome material by the plants because of the difficulty in separating one season's material from another. Values for *Spartina* rhizome production cannot be found in the literature (Keefe 1972), but recent work by Reimold (1972) in the Georgia marshes indicates that the underground standing crop biomass of roots and rhizomes may be more than 2.5 times greater than the standing crop of grass.

Animal respiration.—Respiration rates of larger animals in the embayment, including shrimp, fish, crabs, and eels, were measured in 5.5-l laboratory tanks of marsh water held at field temperature in the dark. The abundant shrimp and common mummichogs, which were present throughout the year, were measured at six temperatures from 3° to 30° C. Less abundant animals that were active only during the summer were measured at 20° C. All the animals were brought directly from the field, placed in the experimental tanks, and allowed to acclimate for 3–5 hr before determinations were begun. Each measurement involved 25–50 shrimp, 9–11 fish, and two to three crabs or eels. Only juvenile menhaden gave any evidence of hyperactivity or other crowding effects. Over 12 replicate measurements were made on random subsamples of field populations of the shrimp and common mummichog, instead of segregating animals on the basis of size, sex, or age. Four to six replicates were made with other species taken in a similar manner. Uptake rates were calculated from data taken over the first 2 or 3 hr, while oxygen concentrations remained above 2.0 mg

/l for fish and 5.0 mg/l for shrimp, levels above which respiration rates appeared to be largely independent of oxygen tension. In the field, concentrations often fell below these levels.

Water used in the measurements was prefiltered to remove planktonic organisms and detritus that may have contributed to the observed oxygen uptake, and a measure of background respiration by the filtered water was taken to correct the observed uptake rates. A layer of plastic film on the water surface prevented diffusion into the tanks. Rates of oxygen uptake were measured continuously with a Yellow Springs Model 54 oxygen meter and self-stirring probe calibrated in marsh water by Winkler determination (Strickland and Parsons 1968).

Plankton metabolism.—Field measurements of photosynthesis and respiration by the plankton community in the marsh embayment were made at least monthly throughout a year; the method described by Strickland and Parsons (1968) was used. Successive short-term incubations of about 4 hr were used throughout each 24-hr period to reduce error from bacterial development on the bottle walls. All determinations were made in triplicate. Water temperatures and salinity were measured with a mercury thermometer and an A.O.Spencer optical refractometer. Solar radiation data were provided by the Eppley Laboratory in Newport, R.I., from a roof-top Eppley pyrheliometer.

Benthic plant metabolism.—Rates of photosynthesis and respiration for the dominant benthic macrophytes in the embayments, *Ulva lactuca* and *Ruppia maritima*, were measured as functions of light energy and temperature in a controlled-environment chamber in the laboratory. Only freshly collected material was used, and all determinations were made in duplicate or triplicate with rates calculated from at least five points. Water taken from Bissel Cove was used and corrected for background metabolism as described for animal-respiration experiments. Oxygen changes were measured continuously with a Winkler calibrated Y.S.I. model 54 oxygen meter. On the basis of evidence presented by Hartman and Brown (1967) and others, that oxygen may be stored internally in the lacunar spaces of many vascular hydrophytes, Wetzel (1965) criticized the use of dissolved oxygen changes in short-term measurements of the metabolism of such plants. If this criticism is applicable to the measurements of *Ruppia* metabolism, the results would be an underestimate of photosynthesis and respiration. Sculthorpe (1967), however, does not make any mention of a well-developed lacunar system in *Ruppia*, and the use of continuous measurements eliminated the possibility of sharp transient changes in oxygen that may result from exchanges between

the internal storages and the surrounding water (Nixon and Oviatt 1972). Radiation measurements in the laboratory were made with a Y.S.I. model 65 radiometer. After the determinations were completed, the plant materials were ovendried at 105°C and weighed.

On several occasions field measurements of the metabolism of *Ruppia* beds were made by enclosing areas of plants and sediment under 0.5-m-diameter plastic domes, one transparent and the other painted black and silvered to reduce heating. Again, changes in oxygen were monitored continuously with the self-stirring probe, and corrections were made for plankton metabolism and sediment respiration as determined from measurements of oxygen consumption by sediment cores in the laboratory and from field measurements under the blackened dome when placed over areas without benthic plants. Following the metabolism measurements, the plant material under the dome was harvested, dried, and weighed.

Sediment respiration.—Oxygen uptake by the top 5–10 cm of sediment from the marsh embayment was measured in replicate 4.5-cm-diameter cores across a range of temperature in the laboratory. In the spring and fall, measurements were taken over 2- to 4-hr periods with the self-stirring oxygen probe. Water over the core was agitated only during a 5-min period every half hour when readings were taken. In general, the method used here was similar to that described by Carey (1967) and others, except that a layer of thin plastic film was used to prevent exchange across the air-water interface. During the summer, measurements were made in the field with the darkened dome used for benthic plant-metabolism studies. Changes in dissolved oxygen in water overlying the sediments resulted from the combined actions of sediment infauna and bacteria, the respiration of organisms associated with large pieces of plant detritus, and from chemical oxidation reactions in the mud. Additional estimates of the metabolic activity of the total sediment community were obtained by subtracting the respiration of larger animals and plankton from measurements of total system metabolism in the embayment taken throughout a year.

Total system metabolism of the embayment.—The small size of the Bissel Cove embayment and the single opening of the embayment mouth for tidal exchange made it possible to regulate the flow of water into and out of the marsh. An inflatable rubber "pig" similar to those used in work on city sewage pipes was fashioned from a large truck tire inner tube on a heavy metal rim mounted between plywood disks. This plug was set in the culvert under the highway bridge crossing the embayment mouth and inflated with a SCUBA tank until it completely filled the passage and cut off all tidal flow. With a known water mass held in the marsh, the single diurnal curve method of Odum and Hoskin (1958) could be used to measure the total metabolism of the embayment.

Since water circulation is often important in regulating the metabolism of aquatic systems, confinement of water during the period of measurement may have introduced errors leading to an underestimate of both production and respiration (Nixon et al. 1971, Nixon and Oviatt 1972). These artifacts, however, would be small compared with similar artifacts long recognized and accepted in bottle experiments with plankton. Clear evidence of an effect of current speed on the metabolism of sediment is still lacking (Hargrave 1969), and it may be that diffusion effects within the sediment are much more important than the thickness of boundary layers in the overlying water. In fact, during a 24-hr period the diurnal curves showed no evidence of consistent change in the rate of production or consumption of dissolved oxygen associated with the amount of time the water had been held in the marsh.

Samples of water were taken in triplicate at least eight times during each 24-hr period (dawn, dusk, midnight, and at approximately 3-hr intervals during the day) and were analyzed for dissolved oxygen by the Winkler technique (Strickland and Parsons 1968). Water temperature and salinity were measured at each interval. Occasional continuous diurnal dissolved oxygen analyses with a Rustrak 190 oxygen-temperature meter indicated that our discrete sampling schedule gave an accurate picture of oxygen changes except during one or two days when the embayment became anoxic late at night. Diffusion rates across the water surface were measured directly with a floating plastic dome and oxygen meter (Copeland and Duffer, 1964, as modified by Hall, Day, and Odum, *unpublished data*), except during the winter when ice covered the embayment and no diffusion correction was used.

The diurnal curves were analyzed by plotting the rates of change in oxygen after correction for diffusion. The area under the positive portion of the rate-of-change curve represents apparent production during the day; the area of negative change is equal to night respiration. Linear extrapolation between the last negative rate-of-change point at dawn and the first at dusk provided a negative area that was attributed to daytime respiration. When added to apparent production, this value gave an approximation of gross production during the day. The procedure of extrapolating rates of dark respiration into the light probably provides a substantial underestimate of gross production, but more direct measures

of this parameter have not yet been developed for field use (Odum, Nixon, and DiSalvo 1969).

Population estimates

Animals in the emergent marsh.—Rough estimates of the abundance of marsh snails, *Melampus bidentatus*, and marsh mussels, *Modiolus demissus*, were taken for preliminary comparison with other marsh areas from counts of twenty-six 0.5-m² quadrats positioned by random toss around the periphery of the embayment. All samples were collected on one day in July. An estimate of the population of fiddler crabs, *Uca pugnax*, was made in early fall by using twenty-two 1-m² quadrats on eight transects through the marsh. Small mammals were checked several times during the year with live traps. A study of the abundant and conspicuous bird populations of the marsh has been described by Lucid (1971), in which 2-hr observation periods were taken at random during the daylight hours twice each week for a 10-month period. With binoculars and a spotting scope, it was possible to observe the entire marsh and make a record of the numbers, species, and activities of all birds in the area every 5 min. This sampling schedule was selected after a continuous month of 2-hr observations made at random times twice each day indicated little day-to-day variation in results. Data collected in this way were supplemented with almost daily spot counts made on trips to the marsh. A study of feeding efficiency and energetics of the herring gull, *Larus argentatus*, a characteristic and abundant bird in the marsh during much of the year, was made on six captured adult birds over a 1-month period. The animals were kept in large cages and fed ad libitum on a diet of trash fish. The birds were weighed during the study, and a record kept of all food consumed and feces produced. Heats of combustion for food, feces, and birds were determined with a Phillipson microbomb calorimeter and a Parr bomb calorimeter, respectively.

Plankton in the embayment.—Counts of diatoms, larger flagellates, and zooplankton were made weekly throughout the summer and occasionally during other seasons. Estimates of phytoplankton were taken from single counts made with a Sedgwick-Rafter cell from 1 liter of freshly collected surface water. Zooplankton samples were collected at three stations in the embayment by pouring measured volumes of water through a #10-mesh plankton net. Single counts of each sample were made on formalin-preserved material.

Benthic plants and sediments.—During June, July, and August, quantitative surveys of benthic plant biomass were taken on four transects across the embayment. A benthic grab sample of 222 cm² area

was used, and four to six samples were collected on each transect. The macro-plants were harvested and ovendried at 105° C. The extreme patchiness of benthic plant distributions made it difficult to arrive at a reliable estimate of plant biomass over the whole embayment, even though an attempt was made to do so by drawing contour maps of plant abundance and measuring them with a polar planimeter. The method probably gives results that are best interpreted as providing a range of plant densities in the area. Field estimates of the relative abundance of algae and submerged vascular plants were kept throughout the year by visually inspecting the embayment bottom through the clear, shallow water and making a weekly note of coverage and density relative to its appearance during the summer when measurements were being made.

A similar sampling program with the benthic grab was used to estimate the amount of macro-detritus (large pieces of dead grass and algae) that was in the surface layers of the embayment bottom. The distribution of this material was more uniform, and the method provided more consistent values of total detrital biomass. An estimate of total organic matter in the sediments of the embayment during summer was obtained by collecting 17 cores of sediment to a depth of 10 cm on transects across the marsh. These cores were divided into 1- or 2-cm-thick layers, dried at 105° C to constant weight, and then ashed at 500°–550° C for 4 hr. A check of the reliability of the ashing oven with eight replicates of a standard sample showed variations of only ± 1% of the mean (69.37% weight loss) regardless of sample position in the oven.

Infauna and epifauna.—Samples of infauna from the embayment sediments were collected weekly from February through July. Up to three grab samples of 173 cm² area each were taken to a depth of 10–15 cm and screened through a 0.5-mm-mesh sieve, and all animals were identified and counted. Dry weights were taken on the total sample for each week. The microbenthic infauna was sampled by Lavoie (1970) during early fall from six locations in the embayment. Single cores of 25 cm² cross-sectional area were removed from the sediment to a depth of 15–20 cm. The volume of each core was measured, and the material was washed through two screens of 1.9-mm mesh and 1-mm mesh. After a thorough washing, confirmed by microscopic examination of material retained on the screens, three 1-ml aliquots of the filtrate were examined for benthic copepods. Three other 1-ml subsamples of filtrate were stained with Rose Bengal to facilitate the counting and separation of nematodes from ostracods and ciliates.

Larger epifauna were sampled 1 or 2 days each

week throughout the year with four pull-up nets maintained around the marsh in a manner similar to that developed by Higer and Kolipinski (1967) for sampling shallow waters in the Everglades. Samples were not collected when thick ice was present during the winter and early spring. The nets used were 1.6 m on a side with a 6-mm mesh and could be pulled through the shallow water to the surface in a few seconds. When resting on the bottom, the nets sank into soft substrate and were nearly invisible from above. Shallow-water animals seem adapted to avoiding danger from above, and the rising nets captured a variety of organisms in great number with a relative abundance in agreement with seine samples.

Grass shrimp.—Population estimates for adults of the abundant grass shrimp, *Palaemonetes pugio*, were obtained in two ways. On four occasions, once during each season, a mark-and-recapture study was carried out following a design developed by Schnabel (DeLury 1951). Large numbers of shrimp were captured with dip nets and small seines, then immersed for about 15–30 sec in an aqueous solution of Alcian blue dye (64g l⁻¹), and counted directly or by volume displacement. Tagged animals were then released over the whole embayment. Checks on marked shrimp kept in the laboratory and in cages in the field showed little mortality due to the tag. In laboratory experiments with adult *Fundulus heteroclitus* and *F. majalis*, the fish would not feed on either marked or control shrimp. Gut analysis of fish in the field did not indicate any differential predation on tagged animals. The mark remained visible throughout the recapture period and often persisted through one molting. On successive days after the first tagging, shrimp were seined from all around the embayment, the number of recaptures noted, the remaining animals marked, and the entire sample returned over the whole embayment. During the winter, when ice prevented seining, the shrimp were dip-netted through holes cut in many places over the area.

A basic assumption of mark-and-recapture techniques is that there is no loss or gain of animals from the populations being measured (DeLury 1958, Cormack 1968). During each marking period a 1-m-diameter, 6-mm-mesh fyke net was placed across the mouth of the embayment, and stone weirs were positioned to channel migrating animals into the trap. The net was moved appropriately to capture flood- and ebb-tide movements. The total numbers of marked and unmarked shrimp entering and leaving the marsh on each tide during the sampling period were always very close, so that there was little net movement in either direction, and any excess in one direction was very small with respect to the total population. The results of the shrimp census were analyzed according to the explicit formula developed by Schumacher and applied by DeLury (1958).

A plot of the shrimp data filled the necessary criterion that the proportion of recaptures in the tth sample be directly proportional to the total number of animals marked and released at the time the sample was taken.

A continuous check of the shrimp population was taken from the once- or twice-weekly counts of animals collected in the pull-up trap nets from four stations in the embayment. Although this method was probably not as reliable as the more elaborate seasonal estimates, the nets caught large numbers of shrimp and gave repeatable results. The movements of shrimp into and out of the marsh were monitored on two flood and two ebb tides weekly with the fyke net described earlier. The estimates of shrimp migration are probably low because of net avoidance and losses to predation in the net.

Fish.—Methods used for estimating populations of fish in the marsh embayment were similar to those used for the shrimp. Four seasonal mark-and-recapture studies were done on the most abundant fish, *Fundulus heteroclitus*, the common mummichog. Fish were captured throughout the embayment with an 18-m, 8-mm-mesh seine and anaesthetized with MS-222. During the winter fish were captured under the ice with baited traps. The anaesthetized fish were marked at the base of the dorsal fin or the caudal fin with a Panjet inoculator loaded with Alcian blue dye in aqueous solution at 64g l⁻¹ (Hart and Pitcher 1969). Mortality experiments in the laboratory and in field cages indicated that the larger fish were not affected by the procedure, but those under 35 mm suffered a high mark mortality. Accordingly, fish below this size were omitted from the marking program. It was assumed that differential predation on the tagged fish was not severe, since the small blue mark was not conspicuous when the fish were active underwater. On anaesthetized animals out of water, the tag was recognizable for 2 months or more. Because of the great amount of time and effort required to tag substantial numbers of fish, only an initial large sample was marked. On subsequent sampling days unmarked and recaptured animals were counted, and the entire sample was returned to the marsh. Recapture samples were taken for up to 4 weeks. Population estimates were calculated from the data with the standard Petersen formula (DeLury 1951).

During the recapture seining and trapping, counts were made of all other species of fish, so that a ratio of their abundance to that of the marked species could be developed. Assuming equal catch-

TABLE 1. Production of emergent plants in Bissel Cove Marsh

| Zone | Area (m²) | Total solar radiation[a] (Kcal yr⁻¹) | Visible radiation[b] (Kcal yr⁻¹) | Aboveground production at the end of growing season | | | | Effi- ciency[d] % |
				g dry weight m⁻²	Kcal g⁻¹ [c]	Kcal m⁻² yr⁻¹	Kcal-yr⁻¹	
Spartina alterniflora (tall)	1.1×10^3	13.5×10^8	6.1×10^8	840	3.3	2.8×10^3	3.1×10^6	0.51
S. alterniflora (short)	12.1×10^3	14.9×10^9	6.7×10^9	432	2.6	1.1×10^3	13.3×10^6	0.20
S. patens	1.4×10^3	17.2×10^8	7.7×10^8	430	3.1	1.3×10^3	1.8×10^6	0.23
S. patens, Distichlis spicata mixture	1.8×10^3	22.0×10^8	9.9×10^8	680	2.8	1.9×10^3	3.4×10^6	0.34
Typha latifolia	3.6×10^2	4.43×10^8	2.0×10^8	693	4.3	3.0×10^3	1.1×10^6	0.54
Total	16.8×10^3	20.6×10^9	9.3×10^9				22.7×10^6	0.24

[a] Eppley pyrheliometer, Newport, R.I.: 12.3×10^5 Kcal m⁻² yr⁻¹.
[b] Calculated as 45% of total (Reifsynder and Lull 1965).
[c] Udell et al. (1969) and Boyd (1970).
[d] (Kcal yr⁻¹/visible radiation)(100).

ability, these ratios were used to extrapolate the results of the common mummie census to give a rough estimate of other, less abundant species.

Movement of fish in and out of the embayment was monitored once or twice weekly with the fyke net and sampling schedule described for the shrimp. Again, the error due to migration was minimal, since the numbers of marked fish entering and leaving the marsh were equal. No net movement of the other species was apparent during the recapture periods. Except during periods of thick ice, a weekly estimate of all fish populations was also taken from the four pull-up trap nets.

THE EMERGENT MARSH

Grass and detritus

The area between the embayment and a fringing wood of white oak trees consisted of 16,800 m² of characteristic marsh grasses, *Spartina alterniflora*, *S. patens*, and *Distichlis spicata*. The distribution of these species, as well as small clumps of cattail, *Typha latifolia*, and *Phragmites communis* is shown in Fig. 2. The *Phragmites* was confined to areas of freshwater input and marked the boundary of the salt-marsh system. As reported in other studies, growth per unit area of *S. alterniflora* was greatest in a 1-m-wide band of tall grass around the periphery of the embayment and along the creek banks and ditches. A shorter form of the same species covered a much greater area and thus contributed more to the overall production of the marsh. The amount of area covered by each plant species, its net production of aboveground parts at the end of the growing season, and its efficiency of production are summarized in Table 1. The 840 g m⁻² yr⁻¹ production of tall *Spartina* in the Bissel Cove marsh has been compared with a summary of production data for other marshes along the Atlantic coast

in Table 2. Apparently the decline in production at higher latitudes is neither as sharp nor as clear as suggested in previous reviews of marsh literature by Cooper (1969) and Keefe (1972) that lacked data for more northern areas.

Production values of the other grasses given in Table 1 agree with measurements reported by Udell et al. (1969) for a number of marshes on Long Island. The 693 g m⁻² biomass of *Typha* was about one-half to one-third of most of the values for this species reviewed by Keefe (1972), but Boyd (1970) has also reported almost identical low values for *Typha* marshes in South Carolina. Tall stands of *Phragmites* along the border of the marsh had 800–1,000 g dry weight m⁻², well within ranges cited by Keefe and reported in an extensive study by Björk (1967) for moderately eutrophic *Phragmites* biotopes.

The efficiency of net production for all grasses on the emergent marsh, 0.24%, is much smaller than the 1.1% annual efficiency of net grass production reported for the Georgia marshes by Teal (1962). Even the value for tall *S. alterniflora* is only about one-half that in Georgia, reflecting the more extreme environment and shorter growing season of the New England marsh. In his study of a Minnesota *Typha* marsh, Bray (1962) reported an aboveground net production efficiency of about 0.8% of visible radiation, a value over three times greater than that for the whole northern salt marsh, and almost 50% greater than for the *Typha* contribution to production on the marsh. As suggested by Teal, high respiratory rates in *Spartina* may reflect the energetic costs of success in the stressed marsh environment and lead to a lower net production efficiency than might be shown by similar communities at the same latitude. Even if Teal's value for *Spartina* respiration (70% of gross production) is ap-

TABLE 2. Biomass of *Spartina alterniflora* (tall and medium)[a] at the end of the growing season in some salt-marsh ecosystems

Marsh location	Biomass (g dry weight m^{-2})
Georgia (Teal 1962)[b]	1,290
North Carolina (Williams and Murdoch 1969)	1,100
Virginia (Wass and Wright 1969)[c]	1,332
Maryland (Johnson 1970)	1,207
Delaware (Morgan 1961)[d]	560
New Jersey (Good 1972)[e]	1,600
Long Island, N.Y. (Udell et al. 1969)	827
Rhode Island (this study)	840
Petpsewick Inlet, Nova Scotia (Mann 1972)[f]	580

[a] Aboveground portions only.
[b] Dry weight taken as 40% of fresh (Williams and Murdoch 1969).
[c] Cited in Keefe (1972).
[d] Size unspecified.
[e] Personal communication.
[f] Calculated from 290 g C m^{-2} yr^{-1}.

TABLE 3. Percentage of area covered by emergent grasses in some marine salt marshes

Marsh location	Species		
	Tall *Spartina alterniflora*	Other *S. alterniflora*	Mixed *S. patens* and *Distichlis*
Georgia (Teal 1962)	20	80	0
North Carolina (Stroud 1969)	6	54	—
Long Island, N.Y. (Udell et al. 1969)	10	67	23
Rhode Island (this study)	7	72	19

plied to the Bissel Cove marsh, the gross production efficiency is still 50% lower than the approximately 1.2% gross efficiency Bray calculated for the cattail marsh using respiration of 15% of gross production. Moreover, recent measurements by Lytle and Hull (*personal communication*) indicate that 70% may be an overestimate of *Spartina* respiration, at least in northern plants. There seems little question that the efficiency of production on the New England marsh is substantially lower than for southern marshes, and perhaps for similar but less stressed systems at higher latitudes as well. The relative coverage of the marsh by each vegetation type has been calculated in Table 3 for comparison with other marshes. A surprising regularity appears all along the coast, even for locations with quite different tidal regimes.

In late summer the *S. alterniflora* flowered and produced great quantities of seed which covered the water in windrows as it was carried back and forth by the tides. The grasses entered a dormant period in late fall and showed no growth until the following spring. This growth pattern is in contrast to that of the southern marsh, where some growth continues all year long. The dead grass remained standing until the thick ice of winter sheared it off and mechanically broke much of it up into smaller pieces during the spring thaw. In southern marshes a similar service may be provided by animals such as the abundant marsh crabs, *Sesarma*, and the fiddler crab, *Uca pugnax* (Crichton 1967). In Georgia marshes Wolf, Shanholtzer, and Reimold (1972) report a mean density in summer of 205 crabs m^{-2}, whereas only 2.7 ± 3.8 per m^2 were found during early fall in this study.

Major export of large pieces of detrital grass came in the spring with the first high tides that followed the ice melt. A smaller "burst" of dead grass export came in February during a brief midwinter thaw. Studies by Schultz and Quinn (*personal communication*) of the export from this system of fine detrital particles suspended in the water indicated a small but much more regular pattern of export throughout the year. Their values for filterable particulate matter in water ebbing from the Bissel Cove marsh were about a tenth of those found in Georgia by Odum and de la Cruz (1967).

Animals

Along with the fiddler crab discussed above, other ground animals were very scarce on the marsh. The values for our summer census of the 26 sample quadrats established around the embayment bank showed a range of 0–60 marsh mussels, *Modiolus demissus*, per square meter with a mean of 5.7 ± 13.2. The marsh snail, *Melampus bidentatus*, was clumped in shaded areas, with a range of 0–300 animals per square meter and a mean of 6.8 ± 60.8. In Georgia Kuenzler (1961) found an average for the marsh mussel of eight animals per square meter with densities four times greater in the most favorable areas along banks. In a study of Virginia marshes made during the fall, Kerwin (1972) reported mean *Melampus* densities of 7.2 animals per square meter. No significant populations of grasshoppers or other insects ever became apparent, in contrast to findings by Smalley (1960) in the Sapelo Island, Georgia, marsh. Occasional small mammals were sighted or trapped, including mice, voles, muskrats, and a raccoon, but they were never present in any number. Their impact on the marsh was probably slight, except for some cutting of *Spartina* for nest building by the muskrat.

THE TIDAL EMBAYMENT

General characteristics

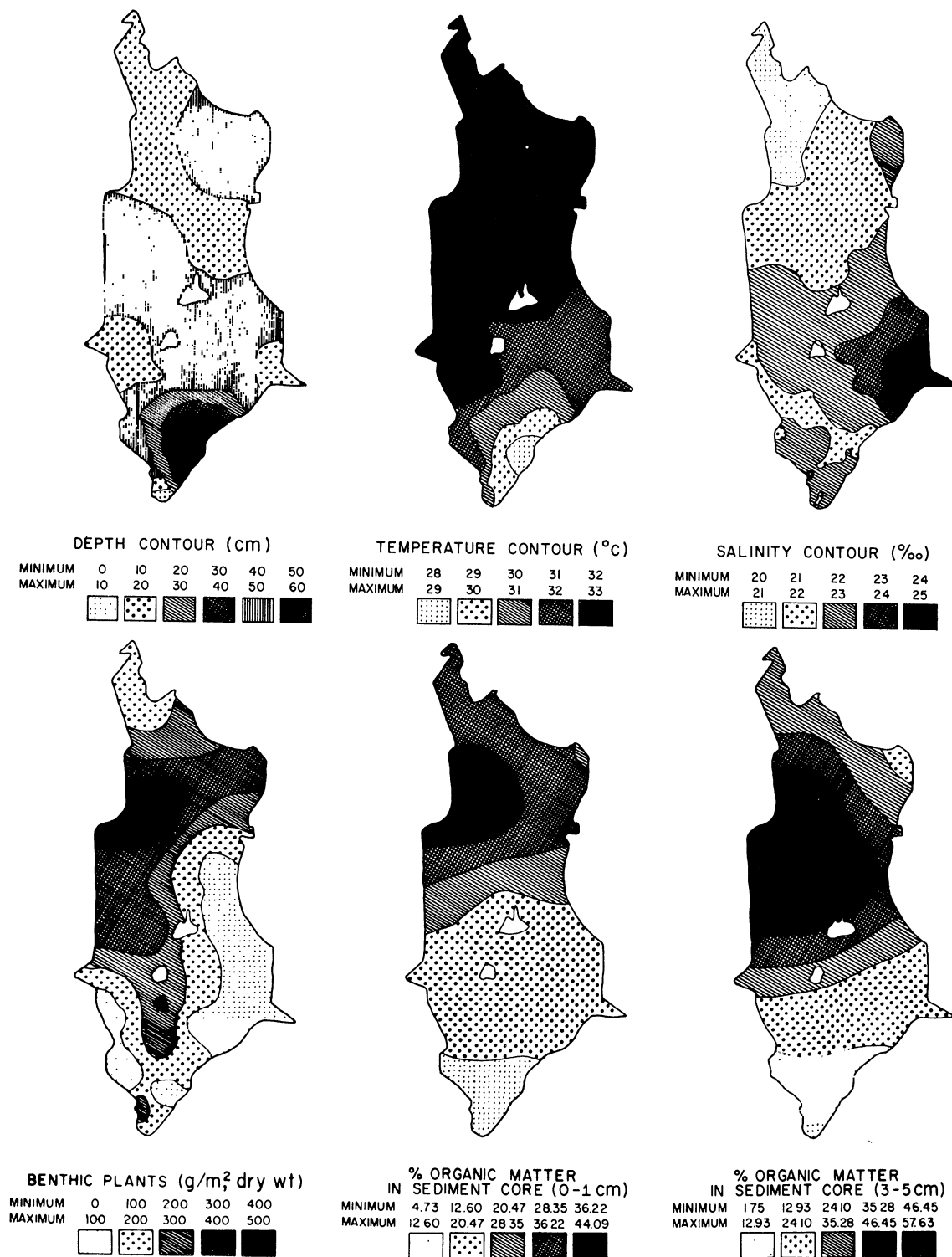As expected for a small shallow tidal embayment, almost all parameters measured showed wide diurnal

DEPTH CONTOUR (cm)

MINIMUM	0	10	20	30	40	50
MAXIMUM	10	20	30	40	50	60

TEMPERATURE CONTOUR (°C)

MINIMUM	28	29	30	31	32
MAXIMUM	29	30	31	32	33

SALINITY CONTOUR (‰)

MINIMUM	20	21	22	23	24
MAXIMUM	21	22	23	24	25

BENTHIC PLANTS (g/m² dry wt)

MINIMUM	0	100	200	300	400
MAXIMUM	100	200	300	400	500

% ORGANIC MATTER
IN SEDIMENT CORE (0-1 cm)

MINIMUM	4.73	12.60	20.47	28.35	36.22
MAXIMUM	12.60	20.47	28.35	36.22	44.09

% ORGANIC MATTER
IN SEDIMENT CORE (3-5 cm)

MINIMUM	1.75	12.93	24.10	35.28	46.45
MAXIMUM	12.93	24.10	35.28	46.45	57.63

FIG. 3. Some characteristic distributions of embayment parameters on a representative June day.

and seasonal variation. The range of variation became more extreme in the most northern and shallow sections of the embayment where small freshwater inflows were present. Over the year, water temperature ranged between −0.5° and 30.5° C with salinities between 1‰ and 28‰. Diurnal variations were least in the winter when daily changes in light and temperature were small compared with
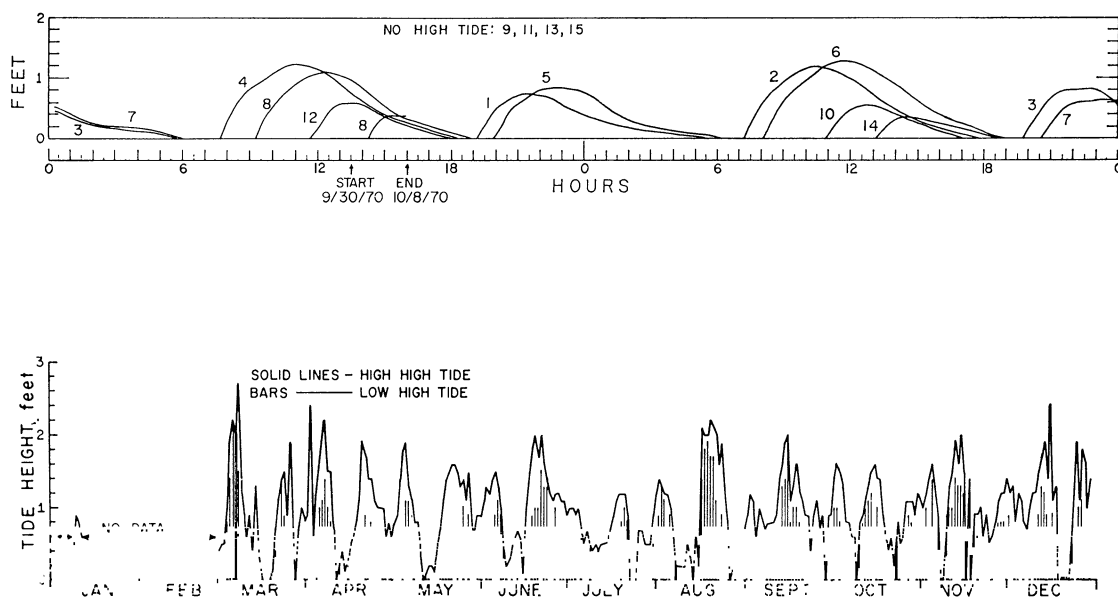
FIG. 4. Top: Daily pattern of the tides in the marsh embayment and the procession of 15 consecutive tides through a week in October. The sill effect completely eliminated high tides 9, 11, 13, 15. Bottom: Seasonal variation in the magnitude of the high tides in the marsh.

hot summer days and cool nights. During summer, ranges of 10°C were often measured over 24 hr. Contour maps of depth, temperature, salinity, sedimentary organic matter, and the biomass of benthic plants on a representative day in June are shown in Fig .3. Because of tidal exchange, ranges of 5°C and 5‰ at any one time were commonly found over the embayment. Benthic plants were distributed in patches. *Ruppia maritima* was most abundant in the lower salinity regions and was replaced by *Ulva lactuca* toward the mouth of the embayment. High densities of both species were often present in limited areas, with up to 500 g dry weight m^{-2}. Both plants went through several periods of rapid growth followed by death and decay and the export of large amounts of detritus. The very high levels of organic matter in the sediment were indicative of the peat-like structure of New England marshes and reflected the importance of the sediment as a storage of detrital material from the submerged plants as well as the emergent marsh grass.

Tidal patterns

The daily rise and fall of water in the Bissel Cove embayment regulates many features of the marsh. The floristic zonation pattern shown in Fig. 2 reflects to some extent the frequency and duration of submergence of the marsh grasses. Though ice prevented operation of a tide gauge during January and February, data for the rest of the year indicated an unusual tidal regime for the marsh. Fill used over the years for the construction and maintenance

of the bridge across the mouth of the embayment had formed a levee, so that tidal inputs to the system were limited to the upper one-third of the tidal cycle. This "sill effect" in the tidal signature is shown for an 8-day period in Fig. 4. The normal semidiurnal tide cycle was apparent only on days when both high tides were greater than the height of the sill. During the time of the study only about two-thirds of all days fell into this category. For such days the yearly average height of the high tide was 0.27 m above sill with a duration of 6.8 hr. The corresponding average for the low high tide was 0.21 m with a duration of 4.7 hr.

The difference in height between the two high tides increased during the spring and early summer, leading into a period from July through October in which there was often only one tide and flushing of the embayment was reduced. There seemed to be no clear seasonal differences in the maximum height of the tides, and the marsh was periodically flushed by several consecutive days of double tides throughout the year (Fig. 4). These modified tidal patterns did not seem to produce unusual features in the marsh, at least as reflected by an analysis of the distribution of indicator species of emergent grasses. The relative amount of area dominated by characteristic grasses in Bissel Cove is similar to values for various other marshes along the coast (Table 3).

Diurnal curves and system metabolism

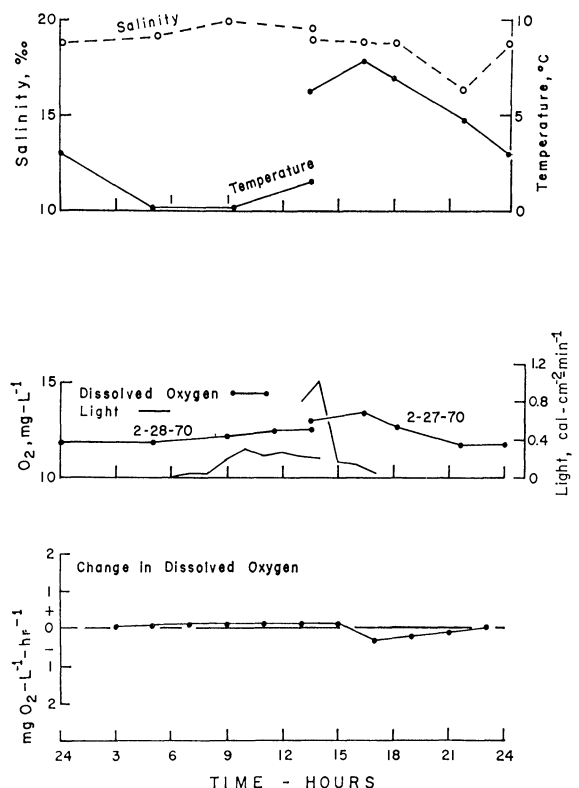The shallowness of Bissel Cove makes it susceptible to large and rapid diurnal and seasonal changes

FIG. 5. Winter diurnal curves of salinity, temperature, solar radiation, and dissolved oxygen in the marsh embayment without tidal exchange.

FIG. 6. Summer diurnal curves of salinity, temperature, solar radiation, and dissolved oxygen in the marsh embayment without tidal exchange.

in dissolved oxygen as well as temperature and salinity that add to environmental stresses from the tides. For representative days in June and February, diurnal curves of these parameters, along with solar radiation, are shown in Fig. 5 and 6 with the embayment closed to tidal activity. Similar curves were collected at least once each month throughout the year to give a measure of total system apparent production and respiration. The magnitude of change increased dramatically between February and March, remained high throughout the summer, then declined again during the following November and December. During the winter the diurnal range was between 1 and 2 mg O_2 l^{-1}; comparable summer values were five times greater. Similar large diurnal oxygen changes have been described by Nichol (1935) for salt-marsh pools in England. Even with the culvert closed on warm summer nights followed by early morning fog, the cove seldom became anoxic, though oxygen values often dropped to less than 1 mg l^{-1}. Throughout the year oxygen curves tended to lag solar radiation by about 1 hr. Rates of apparent production by the entire marsh embayment system are plotted as a function of light energy in Fig. 7. Although the photosynthetic response of
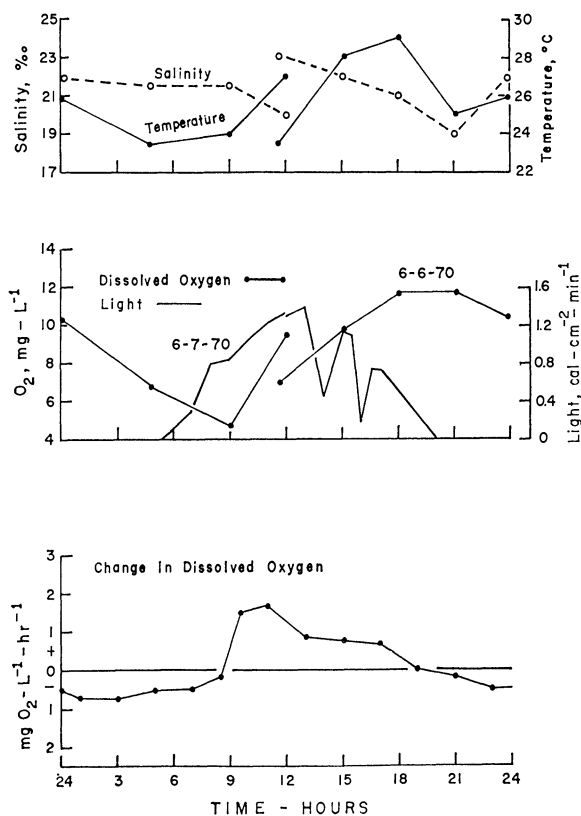
individual plants to increasing light intensity is hyperbolic, a linear relationship provided the best fit to these data for the whole embayment, perhaps because the response of natural communities is complicated by the layering of photosynthetic pigments and the gearing of respiration to temperature and oxygen concentration. The fit is surprisingly good in spite of some scatter and indicates that primary production in the embayment is largely determined by light levels. Seasonal effects of population abundance and composition were less important. Similar findings were reported for sediment algae in the emergent marshes of Georgia by Pomeroy (1959). Data for the two smaller ponds fell within the range of values for the main embayment, indicating that their levels of metabolism were similar.

At night, when measurement of the respiration of the total embayment was possible, rates of oxygen consumption were an exponential function of water temperature (Fig. 8). The consumption of organic matter each night was also closely coupled with the production during the previous day, but with night respiration most often exceeding apparent production during the day. Fourteen points show a production-to-respiration ratio of less than 1, while only
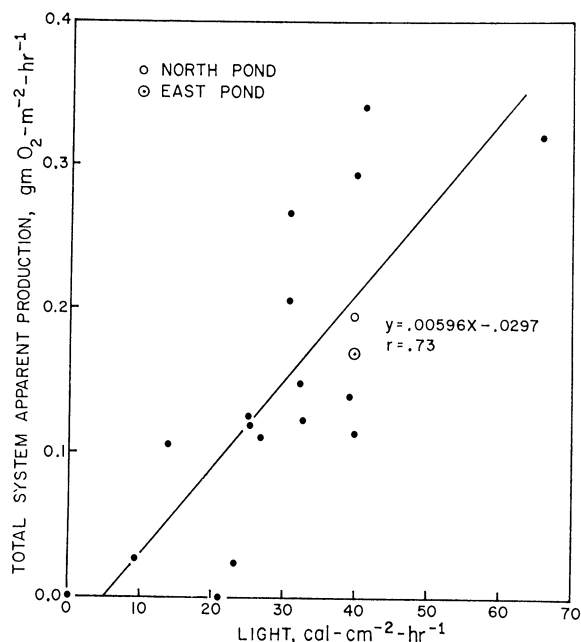
FIG. 7. Rates of apparent production during the day by the total embayment system as a function of solar radiation.

5 days had a P-to-R ratio greater than 1 (Fig. 9) indicating some net production over 24 hr. Values for total system apparent production during the day were less than 1 g O_2 m^{-2} day^{-1} October through February, then rose to a summer level of 2–3 g O_2 m^{-2} day^{-1} that remained relatively stable. Gross production ranged over the year from almost zero in midwinter to summer values of 5–6 g O_2 m^{-2} day^{-1}. Rates of calculated gross production reached 0.6 g O_2 m^{-2} hr^{-1}, but were usually between 0.2 and 0.45 g O_2 m^{-2} hr^{-1}. The seasonal pattern of total system metabolism, including gross production, apparent production, and respiration is summarized with data on light energy and water temperature in Fig. 10. The efficiency of gross production for the entire embayment community averaged 0.80% of visible solar radiation, with a low of 0.12% in November and a high of 1.56% in August. These values place the marsh embayment between very low production systems such as deserts, tundra, and subtropical ocean waters where efficiencies may be about 0.1%, and fertilized systems with high production and large storages, such as algal cultures, sugar cane, and water hyacinths, where gross efficiency may be 4% or more (Odum 1971). If Teal's (1962) value of 70% of *Spartina* gross production used in plant respiration is applied to the grass production at Bissel Cove, then a gross production efficiency of 0.8%, the same as for the embayment, results.
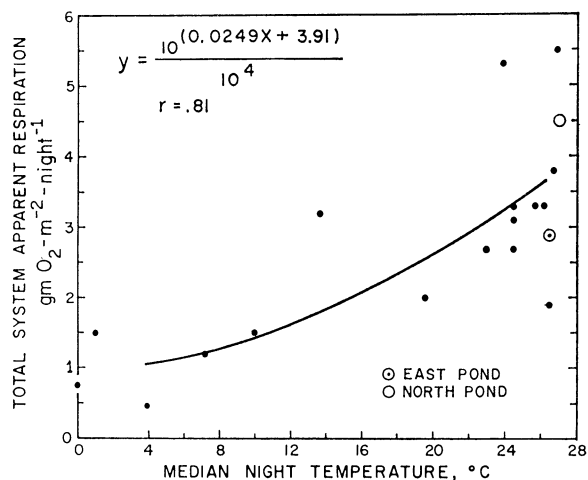

FIG. 8. Rates of night respiration by the total embayment system as a function of water temperature.

Plankton

Phytoplankton photosynthesis and respiration by phytoplankton and zooplankton in the embayment accounted for a relatively constant 10–20% of the total metabolism. Their importance increased during the winter when low temperature slowed sediment metabolism and the water entering the marsh from Narragansett Bay contained large plankton populations from the winter bloom characteristic of this region (Smayda 1957, Pratt 1965). Apparent production by the plankton community ranged from
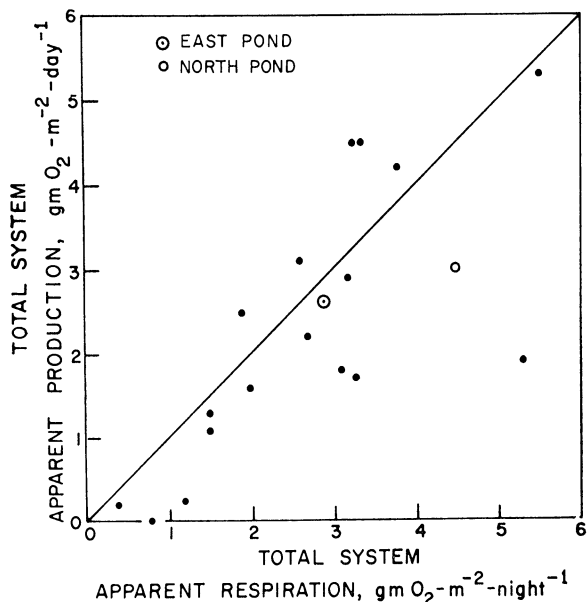

FIG. 9. The coupling of night respiration to production during the previous day in the marsh embayment. The diagonal line represents a P-to-R ratio of 1.
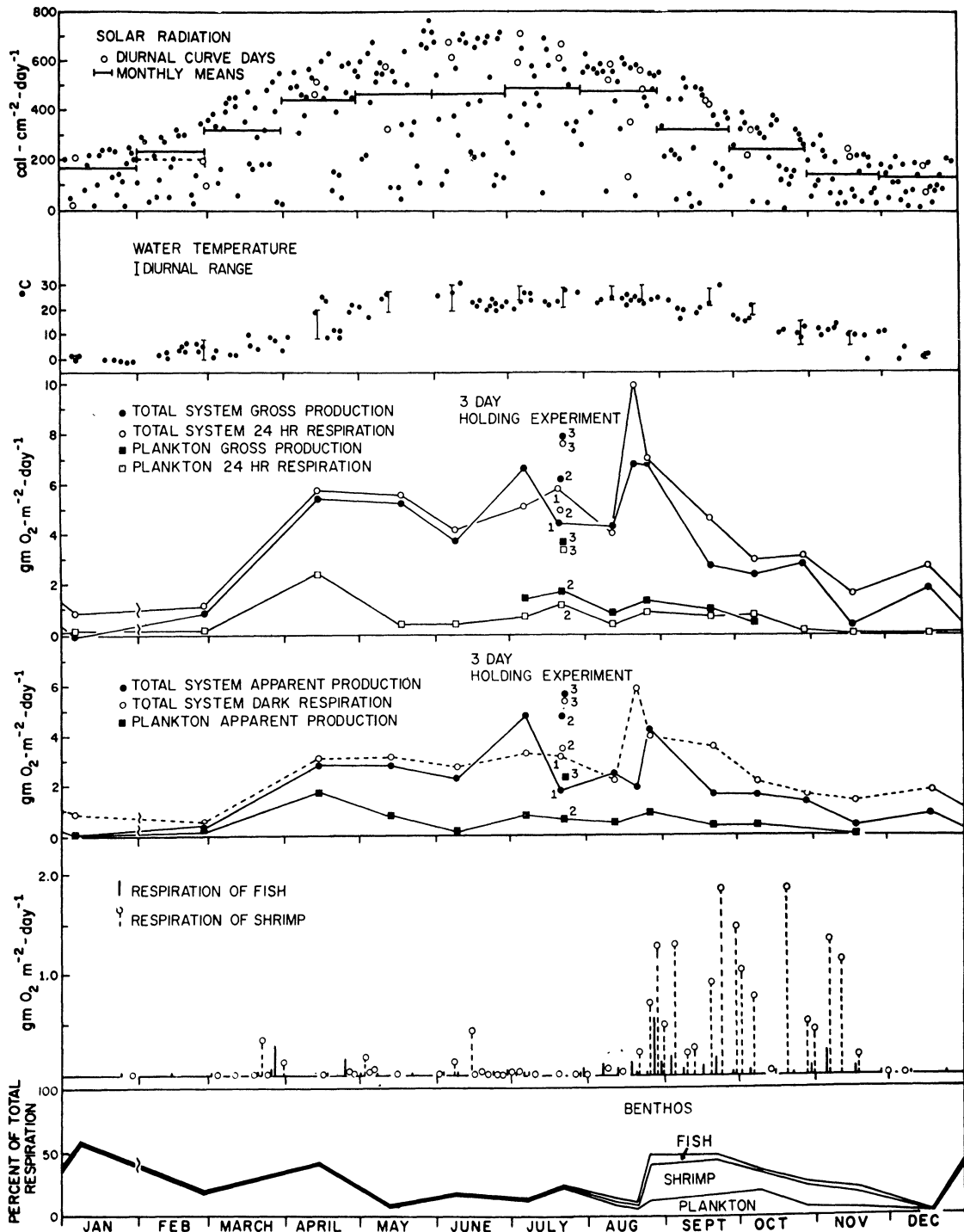
Fig. 10. Annual patterns of solar radiation, water temperature, total system metabolism, and fish and shrimp respiration in the marsh embayment.

zero to a maximum of 2.2 g O_2 m^{-2} day^{-1} with a yearly mean of 0.8 g O_2 m^{-2} day^{-1}. Respiration values ranged from 0.05 to 2.4 g O_2 m^{-2} day^{-1} with a mean of 0.6. Gross production and respiration by the plankton are shown as functions of light energy

and water temperature in Fig. 11. The substantial amount of scatter in the data reflects the erratic nature of plankton abundance in the marsh and indicates the importance of factors other than light and temperature in regulating plankton metabolism.
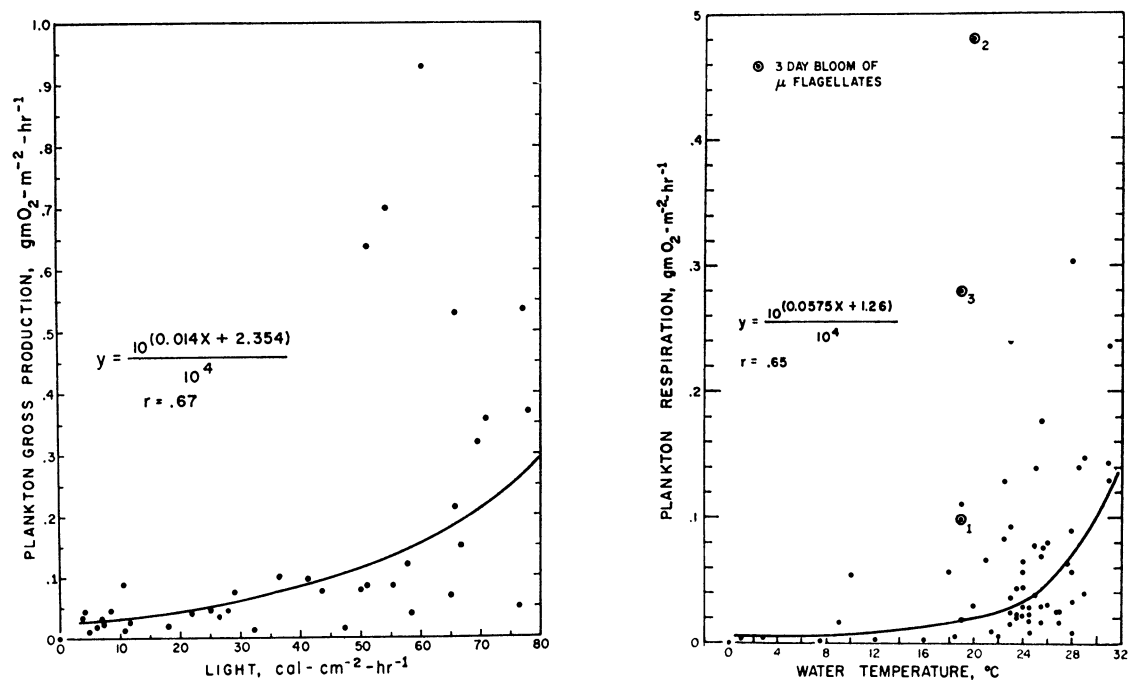
FIG. 11. Plankton gross production (left) and respiration (right) as functions of solar radiation and water temperature. The scatter reflects large and rapid changes in the plankton populations throughout the year, as well as variation in factors such as nutrient levels and species composition.
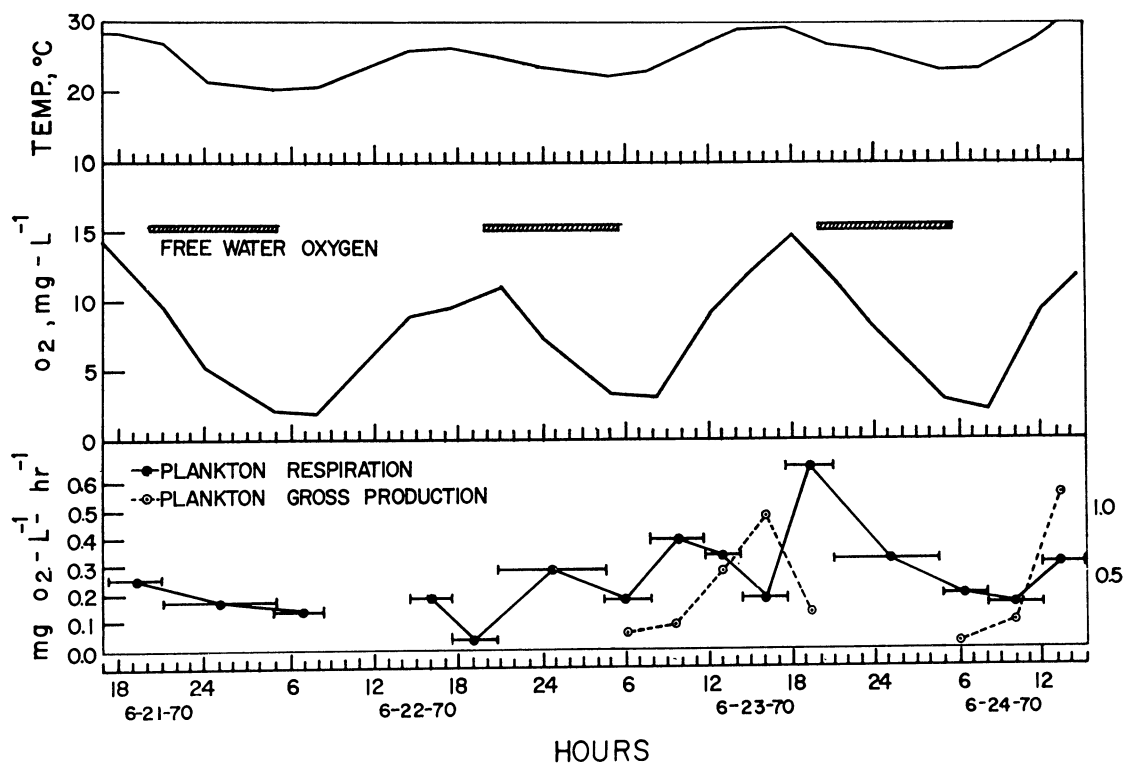

FIG. 12. Three-day holding experiment when tidal exchange was eliminated. Dissolved oxygen patterns remained relatively stable while water temperatures and plankton metabolism increased slightly. The bars on plankton metabolism indicate the period of measurement.
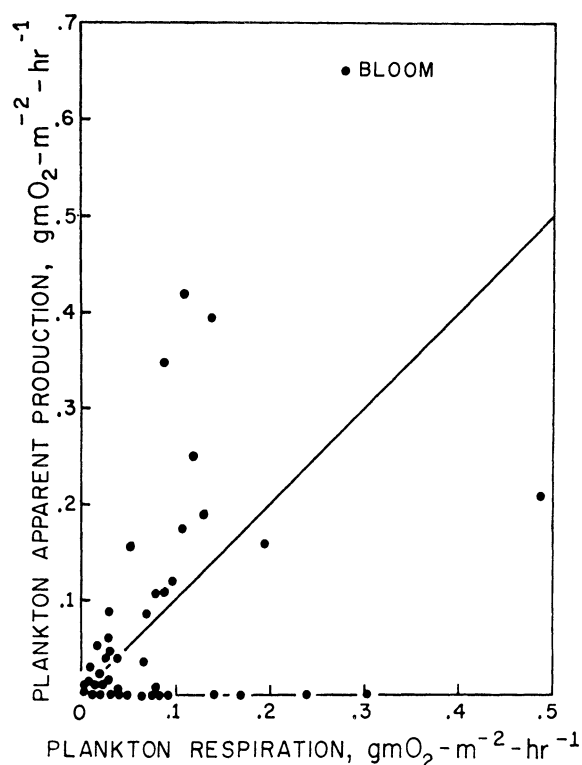
FIG. 13. The coupling of plankton respiration and production in light-dark bottle measurements in the marsh embayment. The diagonal line represents a P-to-R ratio of 1 for the measurement period. On many occasions plankton populations showed substantial net production.

Visible blooms of both phytoplankton and zooplankton were frequent, particularly during the summer, and oscillations were caused by successive cloudy days, cool nights, exceptionally high or low tides, and other sharp changes in the environment. For example, a large bloom of phytoplankton was generated in the embayment during a holding experiment when tidal exchanges were stopped for 3 consecutive days in June when weather conditions were stable. On the other hand, the movement of large schools of juvenile menhaden into the marsh in late summer almost completely eliminated plankton from the water for days at a time. Increasing levels of plankton metabolism during the holding experiment are shown in Fig. 12 along with dissolved oxygen and water temperature. The effect of reduced flushing in increasing total system metabolism is shown in the summary data of Fig. 10.

The respiration of the plankton in the marsh at any one time has been plotted with the corresponding rate of apparent production in Fig. 13. In contrast to studies by Ragotzkie (1959), who found P-to-R ratios consistently less than 1 for the metabolism of plankton in Georgia marsh waters, over

TABLE 4. Plankton production and respiration in some salt-marsh-influenced areas

System	Production (g O_2 m^{-2} yr^{-1})		Respiration (g O_2 m^{-2} yr^{-1})
	Gross	Net	
Georgia estuary-Forks data[a] 3–5 m	1,426	648	803
North Carolina estuaries[b] 1.2 m	199	105	94
Long Island salt-marsh creeks[c] 2 m	251		
Rhode Island marsh embayment[d] 0.25 m	389	180	244

[a] Ragotzkie (1959). Carbon data from Table 2 averaged, pro-rated over a year, and multiplied by 2 to give oxygen.
[b] Williams (1966). Data multiplied by 2 to convert to O_2.
[c] Udell et al. (1969).
[d] This study.

one-half of all the data for the Bissel Cove embayment lie above the line indicating a P-to-R ratio of unity. Integrated values of plankton production and respiration in this system over the year are given in Table 4 for comparison with levels of plankton metabolism in other marsh areas. Our results indicate that while the plankton community of the salt marsh area appears to be a heterotrophic system living on organic imports from the emergent grass areas, it is capable of substantial levels of net primary production at certain times of the year.

Changes in the approximate size of phytoplankton and zooplankton populations during the summer are shown in Fig. 14. Diatoms such as *Asterionella*, *Thalassiosira*, *Nitzschia*, *Skeletonema*, and *Chaetocerus* dominated the larger phytoplankton at all times except during July, August, and part of September, when flagellate species were most abundant. Smaller forms of phytoplankton were not observed in the fresh, whole water samples. In terms of abundance and composition, the phytoplankton of the marsh closely resembled the patterns shown in Narragansett Bay (Smayda 1957, Pratt 1965). Zooplankton densities were usually low, and the population was dominated by benthic harpacticoid copepods. Calanoid copepods such as *Eurytemora*, *Acartia*, and *Oithona* were more abundant in deeper water at the mouth of the embayment.

Benthic plants

Extensive underwater meadows of *Ruppia maritima*, a submerged vascular plant, and *Ulva lactuca*, a green alga, developed quickly in the embayment during summer. Smaller patches of both species were present intermittently at other times of the year. Occasional blooms of *Enteromorpha* appeared
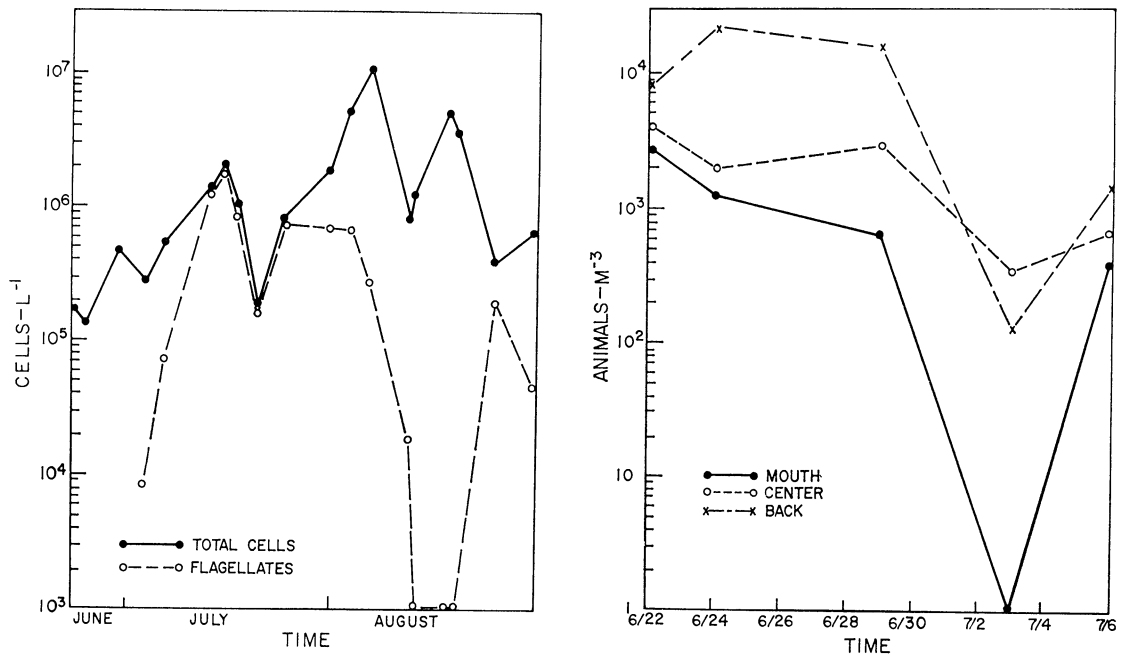
FIG. 14. Single-count estimates of phytoplankton and zooplankton during summer in the marsh embayment. Rapid short-term fluctuations in both populations occurred throughout the year.

during the spring and summer. The total density of benthic plants shown in Fig. 3 was highest in the rich organic sediments near the back of the embayment. The distribution of *Ruppia*, a brackish water species, reflected the input of a small stream in this area of the marsh. In June, a period of rapid growth, densities in the *Ruppia* bed ranged from 48 to 550 g dry weight m^{-2}, then peaked in July at 180–1,460 g dry weight m^{-2}, and declined in August. At the end of July, values of 80–160 g dry weight of dead *Ruppia* were found being carried out of the embayment on ebb tides. The growth of *Ulva* and *Enteromorpha* was confined to areas near the embayment mouth with higher and more constant salinities. At their peak, densities in the algae patches reached 260–600 g dry weight m^{-2}. Although production of submerged plants in the embayment was usually lower than that shown by the grasses on the emergent marsh, the maximum biomass of *Ruppia* per unit area was almost twice that of the fringing tall *Spartina*. The great abundance of these plants provided a substrate for a rich and diverse assemblage of epifauna and may serve as an important source of detritus for the estuary.

Photosynthetic rates in the plant beds were very high because of the large biomass and high light intensity that penetrated the shallow water. The results of laboratory measurements of apparent photosynthesis and respiration at varying levels of light and temperature for *Ruppia* and *Ulva* from the

marsh are shown in Fig. 15. *Ruppia* showed higher rates for each process, but it appears that under field conditions both species quickly become light saturated. Several field measurements in the plant beds under plastic domes showed rates of production and respiration that were very close to those found in the laboratory.

Sediments

The bottom of the Bissel Cove embayment consisted of very soft sediments containing large amounts of detrital organic matter. The organic content of sediment cores ranged from about 4% to over 50%. The highest values were found 3–5 cm below the surface and in the back of the embayment near the entrance of the small freshwater stream (Fig. 3). Lowest values for sediment organics were found near the mouth of the embayment, where fill from the bridge added a large amount of sand, and faster water movement from tides coming over the sill kept fine grain sediments from being deposited. Although submerged plants probably made a contribution to the organic detrital storage, examination of the sediments revealed large amounts of recognizable *Spartina* rhizomes distributed in small pieces throughout the cores. The standing crop of dead *Spartina alterniflora* detritus lying on the bottom of the embayment ranged from 100 to 900 g dry weight m^{-2} with an average of about 200 ± 86 g m^{-2}. Again, most of this detrital material appeared to be
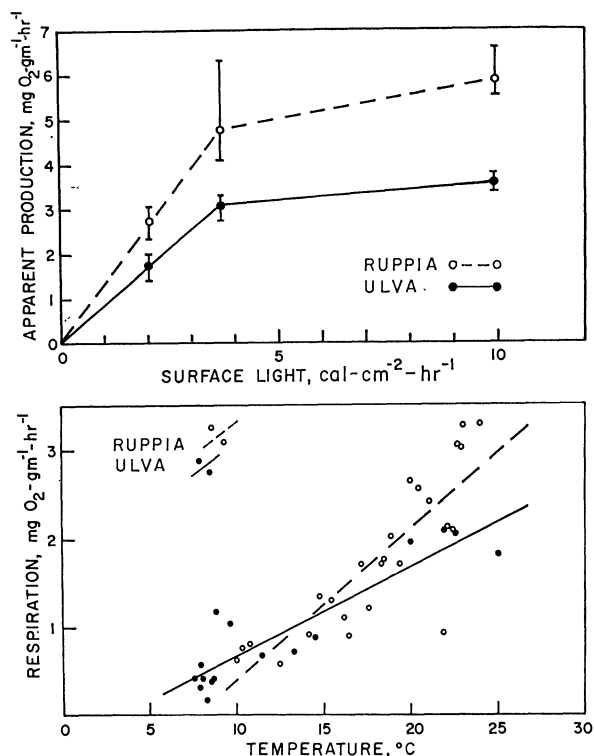
FIG. 15. Photosynthetic and respiratory rates for *Ruppia* and *Ulva*, the dominant macrophytes in the embayment. The bars in the top figure are ranges for three or more determinations. The bottom lines were fit by least-squares linear regression.

TABLE 5. Number and biomass of frequent infauna in the Bissel Cove embayment[a]

Infauna and location	Number (m^{-2})	Biomass (g dry weight m^{-2})
Embayment mouth[b]		
Neanthes	63 ± 79	
Streblospio	79 ± 101	
Polydora	153 ± 223	
Capitella	394 ± 375	
Corophium	2,028 ± 2,765	
Polychaete	176 ± 207	
Total		5.9 ± 3.3
Back marsh[c]		
Capitella	788 ± 1,607	1.1
Nematodes	4.9 × 10^6	0.6
Harpacticoid copepods	4.6 × 10^4	0.05
Ostracods	2.7 × 10^4	
Ciliates	1.8 × 10^5	

[a] Mean ±1 standard deviation: N = 15 or more.
[b] Occasional species: *Mercenaria, Modiolus, Mya, Nereis, Scolecolepides, Euplana, Nematostella,* chironomid.
[c] Occasional species: polychaete.

other sediments in the emergent salt marsh reported by Duff and Teal (1965). These higher rates of metabolism may reflect the rich input of detrital fuels to salt-marsh sediments, in comparison with the plankton rain of sinking cells and fecal pellets that must feed the bottoms of lakes, rivers, and estuaries.

Infauna and epifauna

The soft sediments of the embayment provided a poor substrate for macrofauna, since no clams, large worms, or other animals were found except in the firm bottom areas near the entrance. The soft muds in the rest of the embayment were dominated by a small worm of the genus *Capitella* and a variety of nematodes, ciliates, ostracods, and harpacticoid copepods (Table 5). The most conspicuous group within the meiobenthos were the nematodes, whose numbers reached 10^7 m^{-2} in some areas. Estimates of nematode populations were similar to values reported by Wieser and Kanwisher (1961) for the emergent marsh sediments of Woods Hole, and by Teal and Wieser (1966) for Sapelo Island, except that maximum values here were five times greater than the maximum in Massachusetts, while the weight of organisms was four or five times smaller. Nematodes in the embayment muds here appear to be substantially smaller than those in the Woods Hole marsh. The great abundance of these organisms in marsh sediment-detritus systems in comparison with other areas is apparent from the summary of nematode population levels in various communities in Table 6.

Larger epifauna included abundant amphipods living in the detritus mat on the surface of the

derived from grass roots and rhizomes, with little contribution from the leaves. No *S. patens* was found in the water or in the embayment sediment.

Measurements of oxygen uptake by the sediment were made in the spring and summer across a range of temperatures. Respiration rates near the middle of the embayment increased from 0.04 g O$_2$ m^{-2} hr^{-1} at 5°–10° C to 0.09 g O$_2$ m^{-2} hr^{-1} at 15°–20° C, whereas rates at the back of the embayment ranged from 0.08 g O$_2$ m^{-2} hr^{-1} at the lower temperatures to 0.13 g O$_2$ m^{-2} hr^{-1} at the higher. Maximum rates of uptake were found on four cores taken from the back region near the stream entrance, where the mean rate was 0.32 g O$_2$ m^{-2} hr^{-1}. The regression equation for spring and summer sediment respiration for all cores was:

$$R \text{ (g O}_2 \text{ m}^{-2} \text{ hr}^{-1}) = (1.57T + 9.7)\,10^{-3} \quad (r = 0.92),$$

where T = water temperature (°C).

This regression describes a line with a larger intercept and shallower slope than that derived by Hargrave (1969) in an extensive survey of benthic community respiration from a variety of marine and freshwater systems. The rates of oxygen uptake by the embayment sediments were similar to values for

TABLE 6. Number and biomass of nematodes in some intertidal and subtidal environments[a]

System	Number (m^{-2})	Biomass[b] (g dry weight m^{-2})	Source
Sandy Beach, Denmark	0.10 – 2.5 (10^5)		Fenchel (1969)
Narrow River, R. I.	0.15 – 12.0 (10^5)	3.3 – 11.8	Tietjen (1966)
Off Plymouth, England	0.5 – 1.8 (10^5)	0.23	Mare (1942)
Off Fladen, England	0.75 – 3.0 (10^6)	0.09 – 0.64	McIntyre (1964)
Off Martha's Vineyard, Mass.	0.5 – 6.8 (10^5)	0.04 – 0.51	Wigley and McIntyre (1964)
Buzzards Bay, Mass.	0.15 – 1.8 (10^6)	0.08 – 0.48	Wieser (1960)
Woods Hole marsh, Mass.	1.4 – 2.1 (10^6)	2.4 – 4.6	Wieser and Kanwisher (1961)
Sapelo Island marsh, Georgia	0.98 – 16.3 (10^6)	0.05 – 1.9	Teal and Wieser (1966)
Bissel Cove marsh embayment, R. I.	1.6 – 10.0 (10^6)	0.21 – 1.0	This study

[a] Modified and extended from Lavoie (1970).
[b] Calculated as 25% of wet weight (Wieser 1960, McIntyre 1964).

bottom with densities up to 0.5 g dry weight m^{-2}. Occasional green crabs, *Carcinides maenas*, appeared in the pull-up nets during summer, but were never abundant. Toward the end of summer juvenile blue crabs, *Callinectes sapidus*, began to appear regularly in densities of about 0.6 animals m^{-2}. They reached maximum numbers in mid-September with over 2.5 crabs m^{-2}; carapace widths ranged between 20 and 50 mm. The respiratory rate of juvenile crabs at summer temperature of 20° C averaged 0.95 mg O$_2$ g dry weight^{-1} hr^{-1} (Fig. 16).

Eels became abundant at various times and locations in the embayment during the summer. Maximum densities of five to six large animals per square meter were occasionally found, but values were usually 0.25 m^{-2} or less. Respiratory rates of eels at summer temperatures averaged 0.80 mg O$_2$ g dry weight^{-1} hr^{-1} (Fig. 16). Gut analysis of eels throughout the summer indicated that their diet

consisted largely of the small common mummichog, *Fundulus heteroclitus*, and grass shrimp, *Palaemonetes pugio*. Occasionally other fish and lumps of grass detritus were found. The eels either left the embayment or burrowed into the mud in the fall and did not appear until the following spring. Blue crabs congregated during the winter in deeper holes near the mouth of the embayment, where over 100 animals were lifted with the dip net at one time in January. The crabs remained a part of the community throughout the following summer.

Grass shrimp

The results of mark-and-recapture studies and pull-up net estimates of shrimp population size throughout the year established that from August through November, and again in early spring, grass shrimp were one of the most conspicuous elements of the embayment (Fig. 17). For the entire embayment, mark-and-recapture estimates with 95% confidence limits were:

	Lower limit	Mean	Upper limit
January	50,000	73,000	139,000
March	831,000	923,000	1,009,000
July	11,000	13,000	17,000
October	1,250,000	1,400,000	1,600,000

Coefficients of variation for the pull-up quadrat nets ranged from 0.43 to 1.95, with a yearly mean of 1.03. The highest variability was found during summer when the animals were scarce. When coupled with their great numbers, high shrimp respiration rates in the warm water (Fig. 16) amounted to about 1.9 g O$_2$ m^{-2} day^{-1}, or almost 30% of the total system fall metabolism. The shrimp made a substantial contribution to the excess of respiration over consumption in the embayment at the end of summer (Fig. 10). The low estimates for the summer population do not include the abundant juvenile shrimp which were too small for the nets. For larger, post-juvenile animals the size-frequency distribution throughout the year is shown in Fig. 18.
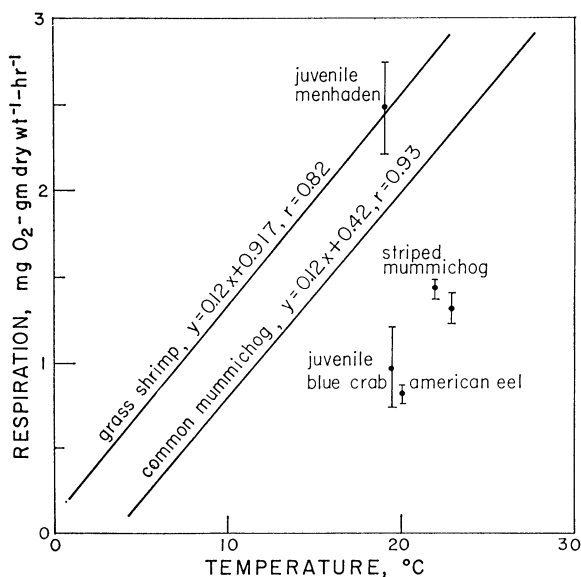

FIG. 16. Respiratory rates for yearly and seasonally abundant larger animals in the marsh embayment. Mean values are shown ± 1 standard deviation.
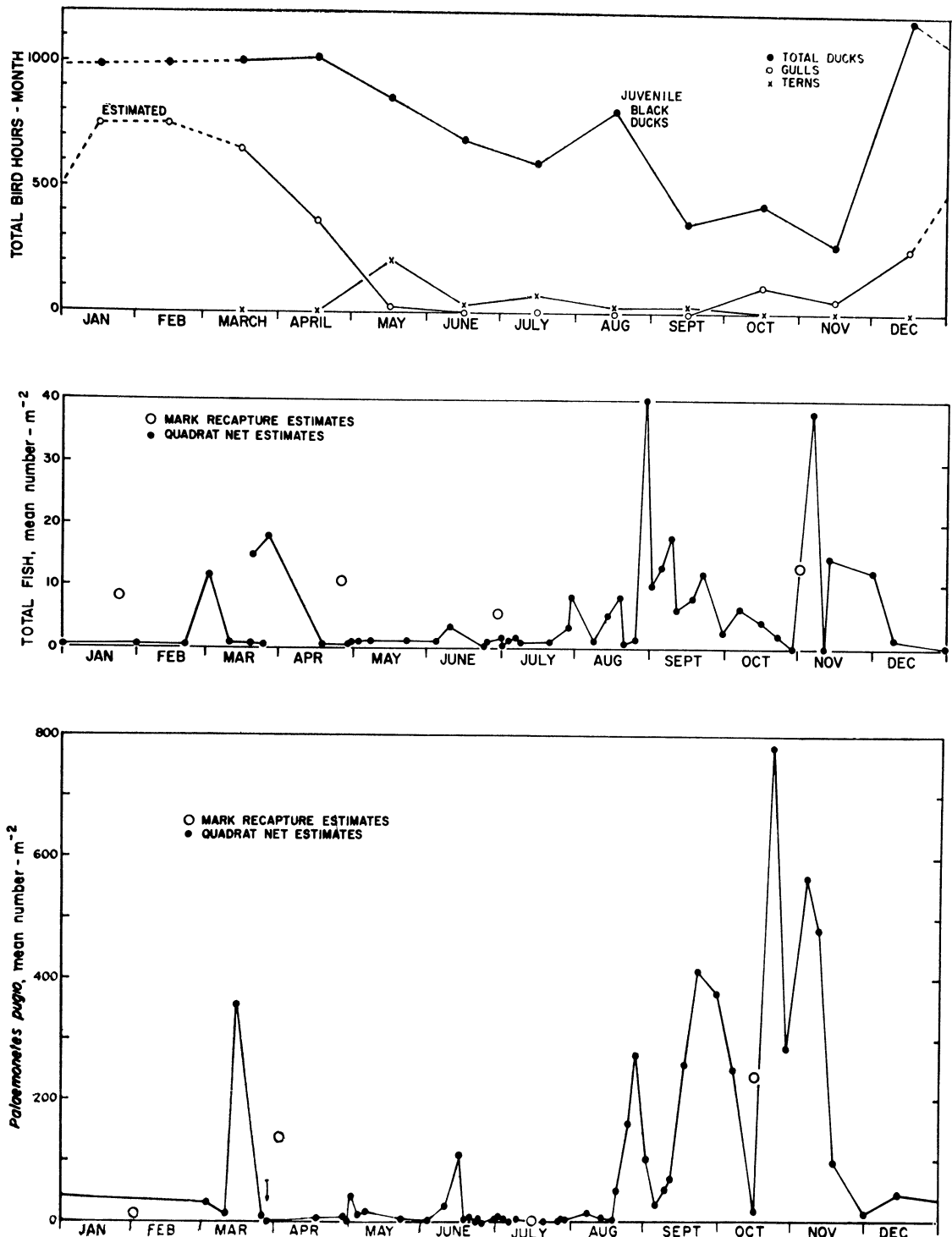
FIG. 17. The abundance of birds, fish, and shrimp throughout the year in the Bissel Cove marsh.

Females averaged 14% larger than males in winter, and up to 30% larger in spring and summer. Rapid growth in both sexes took place from mid-July to mid-October. There was little or no growth from this time through winter until the end of April, when a second growth spurt, especially evident in the females, began.

The movement of shrimp in and out of the marsh largely reflected the abundance of animals in the embayment. Records of shrimp migration through-

out the year are shown as part of Fig. 19. The massive movements of the fall season corresponded to maximum population sizes and spring tides. With the highest tides, up to 40% of the population moved during each cycle. Even during this period, it appeared from tagged animals in the mark-and-recapture study that the population within the embayment was a real entity that moved in and out of the area. Movement in both directions seemed coupled during the fall, but in the rest of the year, movement into the area almost always substantially exceeded emigration. Though some massive mortalities did occur during heavy ice periods in the winter, many of the shrimp moving into the marsh, and most of the animals produced in the embayment itself, probably were consumed by fish and birds in the marsh. There is no evidence to indicate that this marsh area served as an important source of shrimp for the Narragansett Bay estuary.

In laboratory aquaria the grass shrimp appeared to be omnivorous, with a nutritional pattern like that of the similar small estuarine shrimp, *Crangon* (Wilcox 1972). Adults of *Palaemonetes* from the embayment survived well on frozen fish and brine shrimp. In both the laboratory and in the field the shrimp were seen picking pieces of *Ulva*, *Ruppia*, and *Spartina* detritus. This feeding activity was probably directed more toward films of microflora, detritus, and bacteria growing on the plants than it was toward the plant tissue itself. Broad (1957) has shown that larvae of the shrimp lived through metamorphosis when fed a diet of plant and animal materials, but died if only given one or the other.

The interaction of the grass shrimp with marsh detritus is more complex than suggested by a simple feeding relationship. Detailed studies of shrimp ecology at this laboratory by Welsh (1973) indicate that the association of shrimp with detritus accelerates the breakdown and decomposition of the plant material. Scanning electron microscope studies of detritus exposed to the shrimp show structural changes in the grass tissue and the presence of well-developed diatom films growing in emptied cell space consisting only of the cellulose cell walls. Control microcosms with marsh detritus but no shrimp did not show these changes, and water over the control detritus was much lower in nitrogen, phosphorus, dissolved organic carbon, and particulate matter. Excretion and fecal pellets produced by the shrimp, along with their mechanical processing and break-up of detritus, may raise the level of nutrients available for development of bacteria and algae on the nitrogen and phosphorus-poor cellulose substrate of dead grass. Work by Ustach (1969) has shown that small additions of nitrogen and phosphorus can increase the consumption of *Spartina* detritus by
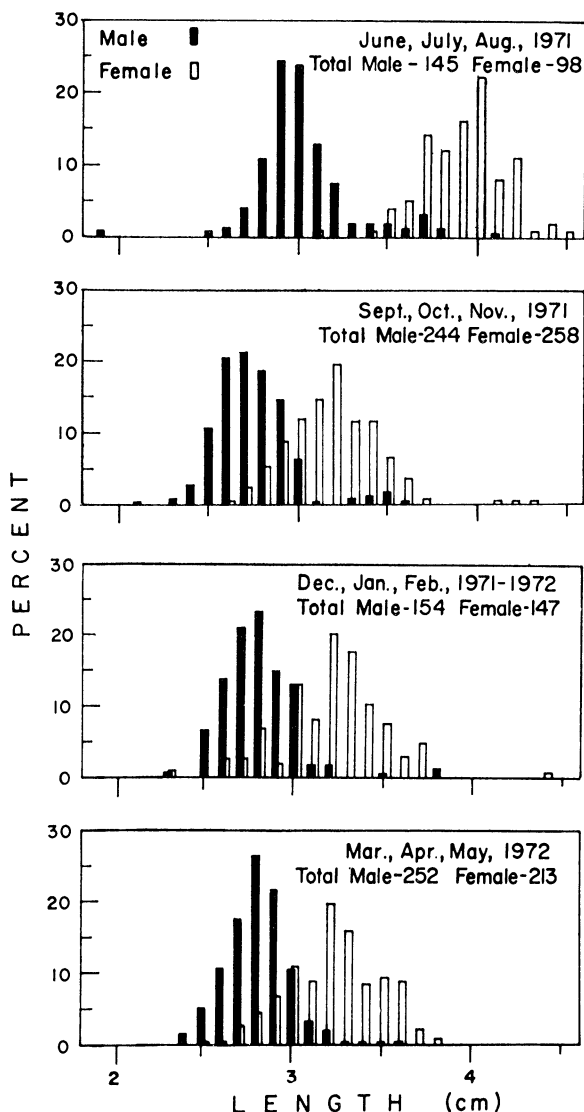

FIG. 18. Seasonal length-frequency distribution of grass shrimp, *Palaemonetes pugio*, in the marsh embayment.

heterotrophs, and Hargrave (1970) has found that changes in the density of a benthic amphipod, perhaps performing a role similar to that of *Palaemonetes*, may accelerate the metabolism of sediment microflora.

Although the shrimp population in the embayment consisted almost entirely of *Palaemonetes pugio*, other small shrimp, such as species of *Crangon* and other *Palaemonetes*, are often common in shallow coastal water (Table 7). One reason for the large, single species populations of *P. pugio* in marsh waters appears to be their tolerance for very low oxygen concentrations that other shrimp cannot survive (Welsh 1973). In waters with higher exchange rates and lower metabolism, dissolved oxygen levels
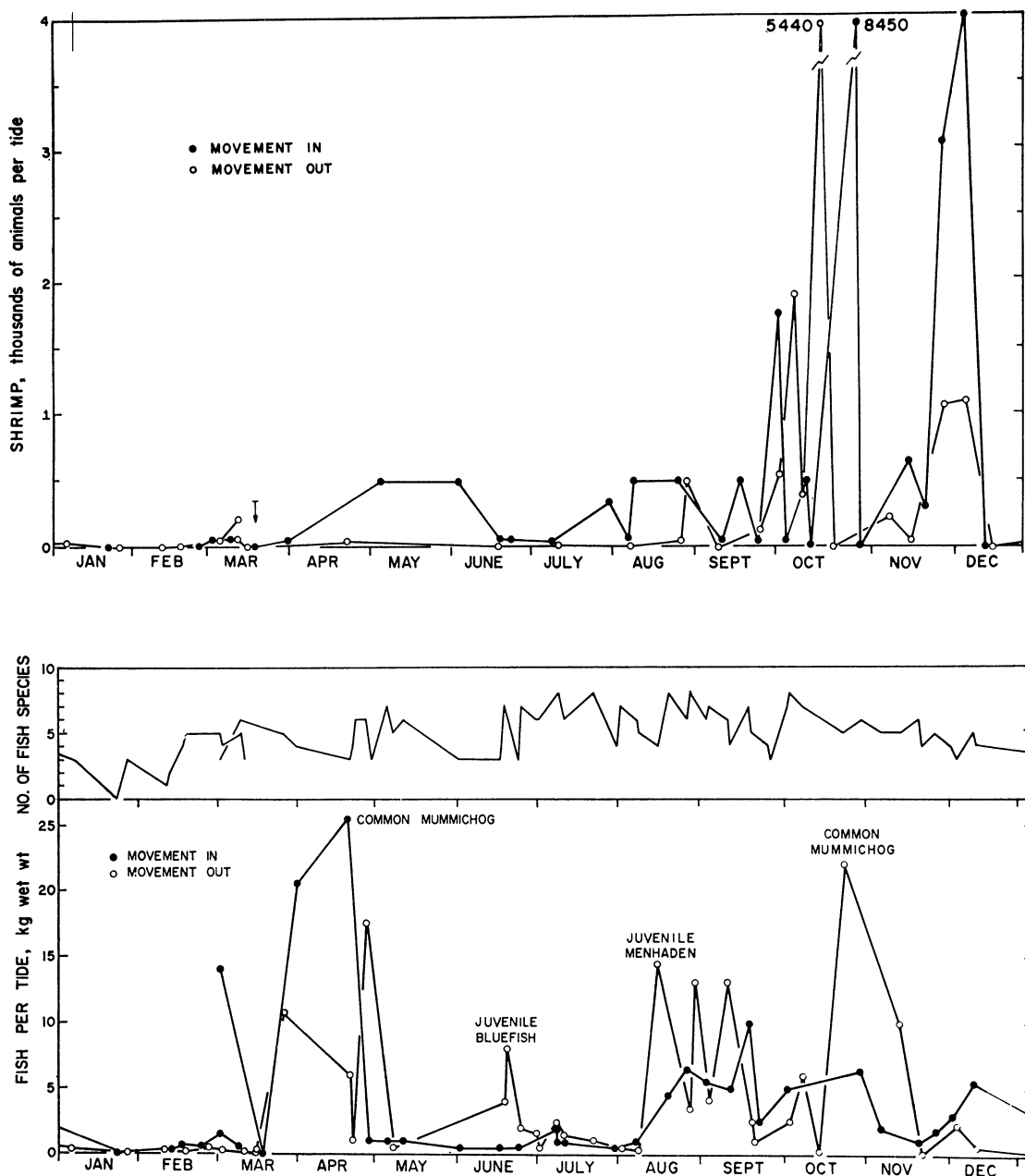
FIG. 19. Seasonal patterns of movement in and out of the marsh by shrimp and fish.

remain higher and other species may successfully compete. Gut analysis in net hauls indicated that shrimp served as a favorite food for fishes with a standard length of 60 mm or more while they were in the embayment, but fish in this size range generally moved out of the embayment during low tides. Since high tide periods averaged only about 6.5 hr each day, and about half of these occur during the dark when many fish cease or reduce feeding, the shrimp escaped intense predation over 75% of the time. Under conditions such as those

in the Bissel Cove embayment, where stresses in the system eliminate competition, predation is minimized, and a positive reward loop is maintained through nutrient exchanges between the animals and their detrital food supply, the biomass of shrimp in the natural marsh system may rival or exceed the shrimp farms of aquaculture (Table 7).

Fish

The shallow water of the marsh embayment contained large numbers of small fish, especially during

TABLE 7. Biomass of shrimp in some aquatic ecosystems

System	Biomass (g dry weight m^{-2})
Turtle grass community, Texas[a]	
Early spring maximum	1.75 (*Palaemonetes pugio*)
Spring maximum	2.55 (Penaeid shrimp)
Commercial shrimp culture, Panama[b]	5.5 – 7.3 (Penaeid shrimp)
Saltwater pond farming, U.S.[c]	14.0 (Penaeid shrimp)
Experimental estuarine pond, N.C.[d]	
Control pond, summer	0.3 (*Palaemonetes pugio* and *P. vulgaris*)
fall	0.2
Sewage pond, summer	2.9 (*Palaemonetes pugio*)
fall	4.1
max. value	9.1
Bissel Cove marsh embayment, R.I.[e]	
Summer	0.1
Fall	15.3 (*Palaemonetes pugio*)
Winter	2.7
Spring	9.0

[a] Hoese and Jones (1963).
[b] Smitherman and Moss (1970) in Sick, Andrews, and White (1972).
[c] Lunz (1967).
[d] Beeston (1971).
[e] This study.

the spring and fall. The yearly abundance of fish from the pull-up nets and the mark-recapture studies is very similar to the abundance pattern of the shrimp (Fig. 17). Because of the greater swimming speed and evasive capability of fish, the two techniques for measuring abundance do not agree as well as they did for shrimp, with the pull-up nets yielding an underestimate of population size. Coefficients of variation for fish in the nets were similar to those for shrimp, ranging from 0.11 to 2.01, with a mean for the year of 1.07. Again, variability was lowest with large fall populations. For the whole embayment the Petersen mark-recapture estimates of fish population sizes, with 95% confidence limits, were:

	Lower limit	Mean	Upper limit
January	49,540	57,000	67,900
April	67,300	75,500	85,900
June	33,000	37,700	43,800
October	79,700	93,000	112,000

During the summer large numbers of juvenile common mummichog were present that were not in-

TABLE 8. Relative abundance of some fish species at each season in the Bissel Cove marsh embayment

Species	Winter	Spring	Summer	Fall
Common mummichog	1.000	1.000	1.000	1.000
Striped mummichog	0.026	0.149	0.247	0.051
Silverside	0.004	–	0.003	0.003
Sheepshead	–	0.021	0.002	0.230
Threespine stickleback	–	0.028	–	–
Mullet			0.001	
Menhaden	–	–	–	0.004
Winter flounder	–	–	–	0.001
Alewife	–	–	–	0.001

cluded in the pull-up nets or tag study for that period.

Twenty species of fish were found in the embayment over the year: seven species in winter, nine in spring, 12 in summer, and 14 in the fall. At all times the common mummichog was the dominant species. Only in the summer and fall, when striped mummichogs and sheepshead minnows made up 20% of the total fish, and in August, when large schools of juvenile menhaden moved into the embayment, were other species conspicuous. At the time of their maximum abundance over 40,000 juvenile menhaden were present in the marsh, as shown by
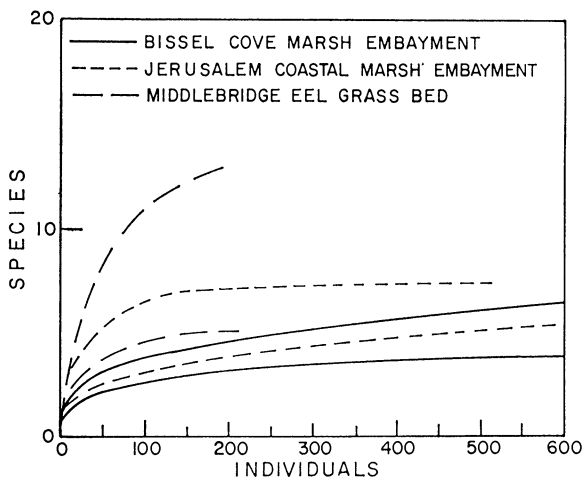

FIG. 20. Range in diversity of fish species from the marsh embayment, an open coastal marsh, and a tidal river eelgrass bed (after Sanders (1968) rarefaction method).

TABLE 9. Seasonal occurrence of fish species in the Bissel Cove marsh embayment

Species	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Fundulus heteroclitus (L.) Common mummichog	×	×	×	×	×	×	×	×	×	×	×	×
Fundulus majalis (Walbaum) Striped mummichog	×	×	×	×	×	×	×	×	×	×	×	×
Menidia menidia (L.) Silverside	×	×	×	×	×	×	×	×	×	×	×	×
Cyprinodon variegatus (Lacepede) Sheepshead	×	×	×	×	×	×	×	×	×	×	×	×
Anguilla rostrata (LeSueur) American eel			×	×	×	×	×	×	×	×	×	
Pomlobus pseudoharengus (Wilson) Alewife			×	×	×	×	×	×	×	×	×	
Mugil cephalus (L.) Mullet						×	×	×	×	×	×	
Brevoortia tyrannus (Latrobe) Atlantic menhaden						×	×	×	×	×	×	
Roccus americanus (Gmelin) White perch						×	×	×	×	×	×	
Pomatomus saltatrix (L.) Blue fish						×	×	×	×	×	×	
Tautoga onitis (L.) Tautog						×	×	×				
Clupea harengus (L.) Sea herring			×	×	×							
Stenotomus chrysops (L.) Scup									×	×	×	
Pseudopleuronectes americanus (Walbaum) Winter flounder									×	×	×	
Scophthalmus aquosus (Mitchill) Window pane flounder									×	×	×	
Hyporhamphus unifasciatus (Ranzani) Halfbreak									×	×	×	
Lucania parva (L.) Rainwater fish						×	×	×				
Gasterosteus aculeatus (L.) Threespine stickleback	×	×	×	×	×							×
Apeltes quadracus (Mitchill) Fourspine stickleback	×	×	×	×	×							×
Pungitius pungitius (L.) Ninespine stickleback	×	×										×

pull-up-net estimates with school densities of over 40 fish m^{-2}. The relative abundance of more common species at each season is shown in Table 8, and the seasonal occurrence of each of the 20 marsh species is summarized in Table 9. The annual species-diversity range in the marsh embayment is compared in Fig. 20 with the annual range of fish diversity in a salt-marsh embayment located on the Rhode Island ocean coast, and with a tidal eelgrass bed in the Narrow River, at the mouth of Narragansett Bay. The diversity within the coastal marsh was highest in the fall, whereas the diversity of fish in the eelgrass bed was highest in late spring. Like most stressed systems, the salt marshes appeared low in diversity, with large numbers of one or two species. These results suggest that the marsh is not used directly by large numbers of outside species as a nursery or feeding area.

Large common mummies were most abundant in spring, when spawning began in late April and continued through June. Size-frequency distributions for the common mummichog at each season indicate that a greater proportion of small fish enter the population in summer (Fig. 21). During winter the young-of-the-year fish were the most dominant group. Gut analysis of the small common mummichog indicated that their rapid growth was supported by a diet that consisted of harpacticoid copepods, amphipods, benthic diatoms, and unidentified bottom detritus, in order of abundance. Miscellaneous items, including fish eggs, worms, isopods, and ostracods, also appeared in some samples. Larger fish of both *Fundulus* species fed largely on the shrimp, *Palaemonetes*, juvenile fish of their own and other species, and detritus. None of the marked shrimp or fish were ever found in the gut analysis. Bio-
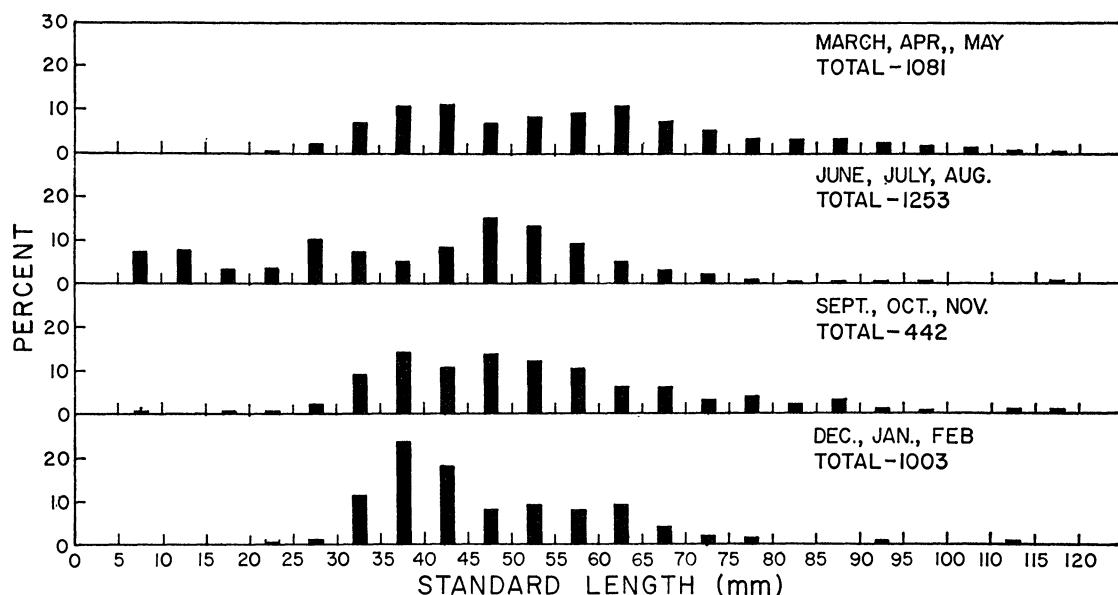
FIG. 21. Seasonal length-frequency distribution of common mummichog, *Fundulus heteroclitus*, in the marsh embayment.

chemical studies of feeding in both *Fundulus* species in the Bissel Cove embayment by Jeffries (1972) indicated that their diets consisted of five parts detritus to one part marine invertebrates. Eels and white perch were voracious feeders on shrimp as well as juveniles and adults of all the other fish species. As mentioned earlier, plankton feeding by the juvenile menhaden was so intense that water in the embayment became almost completely clear. Most, if not all, of their consumption was probably used in maintenance metabolism. Their respiratory rate (Fig. 16) was higher than that of other marsh animals, and their guts were almost always empty. The menhaden did not appear to grow at all during their stay in the marsh, and the heat of combustion for the Bissel Cove juvenile menhaden tissue (Table 14) is significantly lower than the 5.1 Kcal g⁻¹ reported by Thayer et al. (1973) for postlarval and adult menhaden in North Carolina. With such poor nutritional conditions, the menhaden probably remained in the embayment only to escape intense predation by large blue fish that were abundant in the bay.

Respiration rates as a function of water temperature for the two species of mummies are shown in Fig. 16. During the fall, with menhaden present, total fish respiration in the embayment was about 0.05 g O_2 m⁻² day⁻¹, with a more representative fall value of 0.01 g O_2 m⁻² day⁻¹. Values were much smaller during the rest of the year. At its peak, fish respiration never exceeded 8% of the total system metabolism in the embayment (Fig. 10). Length-weight regressions developed for calculating fish biomass when coupled with wet-dry weight conversions are summarized in Table 10 for the major species in the embayment.

Total fish movement in and out of the marsh (Fig. 19) was approximately equal over the year. During the large migrations of common mummichog imbalances did occur when great numbers of fish moved in with the spring, then emigrated in the fall. This activity by the very abundant common mummichog was responsible for the strongly bimodal pattern of fish activity compared with that of the shrimp. Other species, including striped mummi-

TABLE 10. Length-weight regressions for some salt-marsh embayment fish

Species	N	Regression[a]	r
Common mummichog[b]	296	$\log W = (0.024L + 0.313)(10^{-4})$	0.97
Striped mummichog	59	$\log W = (2.76 \log L - 1.36)(10^{-3})$	0.97
Menhaden	85	$\log W = (0.0112L + 4.01)(10^{-4})$	0.73
American eel	38	$\log W = (2.94L + 0.326)(10^{-3})$	0.96
Sheepshead	22	$\log W = (1.2 \log L(10^{-6}))$	0.99
Juvenile blue fish	104	$\log W = (0.0403L + 1.44)(10^{-3})$	0.81

[a] Where W = wet weight (g) and L = standard length (mm).
[b] Dry weight (g) = 0.21 W + 0.074.

TABLE 11. Biomass of fish in some aquatic ecosystems

System	Biomass (g dry weight m^{-2})	Source
Coral reef Bermuda		
Summer	12	Bardach (1959)
Turtle grass community, Texas		
Summer	0.08 – 0.5	Hoese and Jones (1963)
Eel Grass community, R.I.		
Summer	0.04 – 0.4	Nixon and Oviatt (1972)
Surf fish, Texas Coast		
Winter	2.9	McFarland (1963)
Summer	11.6	
Demersal fish, Long Island Sound		
Summer	0.76	Richards (1963)
Experimental estuarine pond with sewage, N.C.		
Fall	4 – 15	Hyle (1971)
Winter	3 – 6	
Summer	3 – 11	
Guadalupe Bay, Texas		
Winter	0.4	Moseley and Copeland (1969)
Spring-summer with menhaden	10	
Bissel Cove Marsh embayment, R.I.		
Summer	0.3 – 8	This study
Late summer with menhaden	28	
Fall	7 – 14	
Winter	5	

chogs, silversides, sticklebacks, eels, and sheepshead minnows were much less abundant (Table 8), and their migration patterns showed small transient peaks at irregular intervals throughout the year. These species also remained in the embayment at all seasons (Table 9). Fish such as the menhaden and juvenile blue fish that showed a strong seasonality also showed marked migration peaks (Fig. 19). Net movements of these less abundant species in one direction or the other were not obvious in the data, but it was not possible from the number of samples available to make a reliable budget because of their small numbers and irregular patterns of movement. Fish movement could not be related in a direct way to water temperature or to tides. Additional attempts to resolve movement in terms of temperature changes and temperature-tide interactions were also unrewarding. Although the biomass of small fish produced and maintained in the marsh embayment compared favorably with that of other systems, (Table 11), the lack of a large clear pulse of net export during the year suggests that the marsh embayment is not supplying great numbers of animals to feed larger fish in the bay.

Birds

A 10-month study of birds in the Bissel Cove marsh in cooperation with Lucid (1971) recorded 27 species during the year, with a high of 16 in July and a low of 5 in March (Table 12). Of this total perhaps only 20 are marsh or shorebirds; the remaining seven are best described as occasional visitors from bordering woodlands and fields.

The seasonal abundance of ducks, gulls, and terns, the three major types of birds using the marsh, is shown with the seasonal patterns of fish and shrimp in Fig. 17. Black ducks and mallards were the heaviest users of the area throughout the year, with mallards most active in spring and summer. Use by gulls and terns also showed a sharp seasonal separation. In winter up to 30 herring gulls at a time were often seen "fishing" through small holes in the ice, but their numbers declined in early spring as the common terns arrived and began wheeling over the marsh to dive for fish. Later in the summer the least tern replaced the common and stayed on into the fall when the herring gulls returned.

No correlation was apparent between use of the marsh by birds and the abundance of plant or animal food in the embayment. The number of birds in the marsh was lowest when fish and shrimp were most abundant (Fig. 17). When present in the embayment, each species devoted different amounts of time that varied with season to feeding activities (Table 13). In general, smaller birds, such as terns, spent a greater proportion of their time in these activities, though food gathering increased to almost 80% of residence time for black ducks in the 2-month period before the hatching of new ducklings in August. Field observation showed that both ducks fed largely on *Ruppia* and *Ulva*, though mallards also were adept at capture of common mummichogs and shrimp. Terns and gulls fed entirely on fish. Laboratory experiments by Lucid (1971) indicated a daily maintenance ration for adult herring gulls of 50.9 ± 3.6 g dry weight of fish per bird, or

TABLE 12. Seasonal occurrence of bird species in the Bissel Cove marsh embayment[a]

Species	Month									
	3	4	5	6	7	8	9	10	11	12
Anas rubripes Black duck	×	×	×	×	×	×	×	×	×	×
Anas platyrhynchos Mallard	×	×	×	×	×	×				
Larus argentatus Herring gull	×	×	×			×		×	×	×
Larus marinus Great black-backed gull		×								
Larus delawarensis Ring-billed gull		×						×	×	×
Larus atricilla Laughing gull						×				
Sterna hirundo Common tern				×	×					
Sterna albifrons Least tern				×	×	×				
Podilymbus podiceps Pied-billed grebe							×	×		
Falco sparverius Sparrow hawk		×								
Ardea herodias Great blue heron		×	×		×	×			×	
Leucophoyx thula Snowy egret				×	×	×				
Butorides virescens Green heron			×	×	×	×	×			
Nycticorax nycticorax Black-crowned night heron					×	×				
Cygnus olor Mute swan					×	×				
Rallus longirostris Clapper rail								×	×	×
Tringa solitaris Solitary sandpiper							×			
Totanus flavipes Lesser yellowlegs			×	×		×	×	×		
Megaceryle alcyon Belted kingfisher	×			×	×	×	×	×	×	×
Tyrannus tyrannus Eastern kingbird				×	×					
Sayornis phoebe Phoebe					×					
Hirundo rustica Barn swallow				×	×					
Corvus brachyrhynchos Crow			×							×
Turdus migratorius Robin			×							
Sturnis vulgaris Starling			×	×	×					
Agelaius phoeniceus Red-wing			×		×					
Quiscalus versicolor Bronzed grackle	×		×		×					

[a] Modified and expanded from Lucid (1971).

17.7% of their dry body weight. Excreta produced amounted to 17.1 ± 4 g dry weight per bird, giving a weight-based assimilation efficiency of 66.4%. By using the measured heats of combustion shown in Table 14, these same data gave an energy-based efficiency of 86%. Even during their maximum abundance, the herring gulls consumed less than 0.5% of the standing crop of fish. Judging from the large amounts of excreta that accumulated at times on winter ice, however, they may be more important

TABLE 13. Percentage of residence time spent in feeding by dominant birds in the Bissel Cove marsh embayment

Species	Month									
	M	A	M	J	J	A	S	O	N	D
Black duck	33	45	—	79	78	6	4	62	0	0
Mallard duck	37	24	25	16	—	—	—	—	—	—
Herring gull	15	13	—	—	—	—	—	25	22	56
Ring-billed gull	—	—	—	—	—	—	—	—	13	28
Common tern	—	—	49	—	—	—	—	—	—	—
Least tern	—	—	—	100	97	75	—	—	—	—

in contributing to algal and microbial dynamics by increasing the supply of available nutrients, a role attributed to gulls living around rock tide pools on the Baltic by Ganning and Wulff (1969).

COMMUNITY ENERGY FLOW

The salt marshes of New England are marked by sharp seasonal changes and short-term swings of temperature, light, and salinity that make the marsh a different place from week to week as species enter and leave throughout the year. A phenological summary of some important changes in the Bissel Cove marsh is given in Fig. 22. Energy-flow diagrams for the marsh system on representative days in summer and winter (Fig. 23) have been prepared from the data presented in previous sections, along with the bomb-calorimetry values for marsh organ-

TABLE 14. Heats of combustion of some component species in the Bissel Cove salt marsh

Material	Kcal g dry weight^{-1} [a]
Plants	
Ruppia maritima	3.24 ± 0.05
Ulva lactuca[b]	1.61
Spartina alterniflora[b]	
Tall–medium	3.22
Short	2.57
Spartina patens[b]	3.08
Distichlis spicata[b]	2.96
Submerged macrodetritus	2.49 ± 0.03
Animals	
Palaemonetes pugio (mixed adults)	4.61 ± 0.03
Fundulus heteroclitus (adult)	
Female with eggs	4.55 ± 0.15
Female without eggs	4.59 ± 0.10
Male in breeding color	4.31 ± 0.10
Fundulus majalis (adult)[c]	
Brevoortia tyrannus (juvenile)	4.37 ± 0.06
Callinectes sapidus (juvenile)	3.07 ± 0.25
Anguilla rostrata[d]	6.4
Mixed amphipods	3.69 ± 0.28
Larus argentatus[e]	5.36 ± 0.05
Gull excretion	2.06 ± 0.18

[a] Mean ± 1 standard deviation, this study.
[b] Udell et al. (1969).
[c] Thayer et al. (1970).
[d] Hunter (1972).
[e] Lucid (1971).
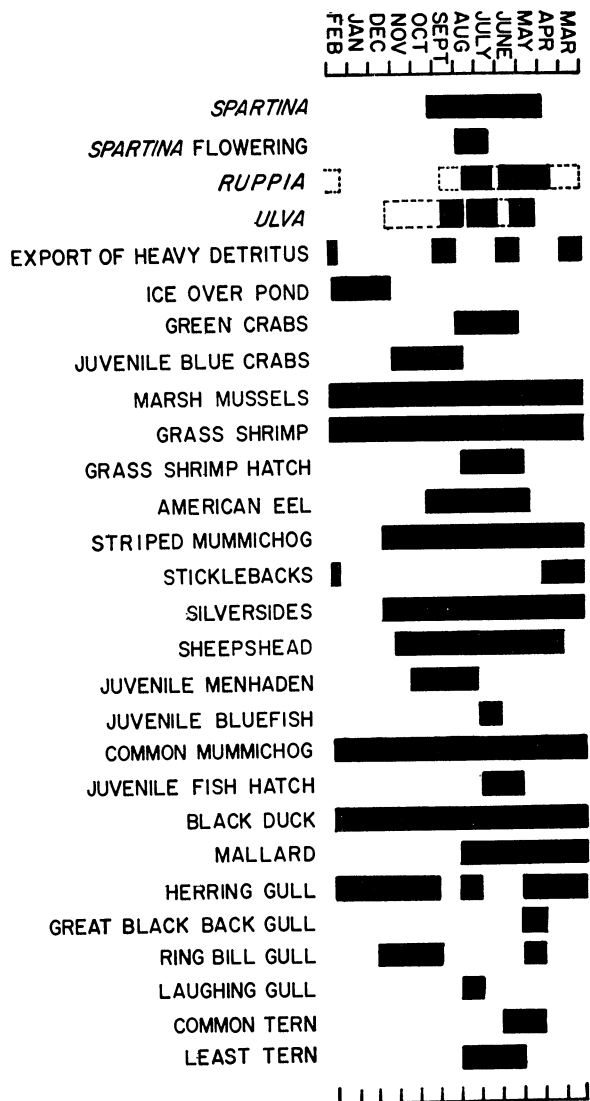
FIG. 22. Phenological summary showing seasonal changes of species composition in the Bissel Cove marsh during the study year.

isms in Table 14. While Teal's (1962) diagram of energy flow at Sapelo Island, Georgia, emphasized the emergent marsh, most of the effort here has been directed toward expanding details of the energy flow in the marsh creeks and embayments that are intimately coupled with the tall stands of grass and serve as tidal pathways linking the emergent marsh with larger estuaries and offshore waters. The diagrams emphasize the great importance of detrital food chains and large sedimentary organic storage in the embayment that agree with earlier findings by the Georgia group for the emergent marsh. They also indicate that large standing crops of plants and animals may be supported in the marsh-embayment complex, and that high levels of primary production
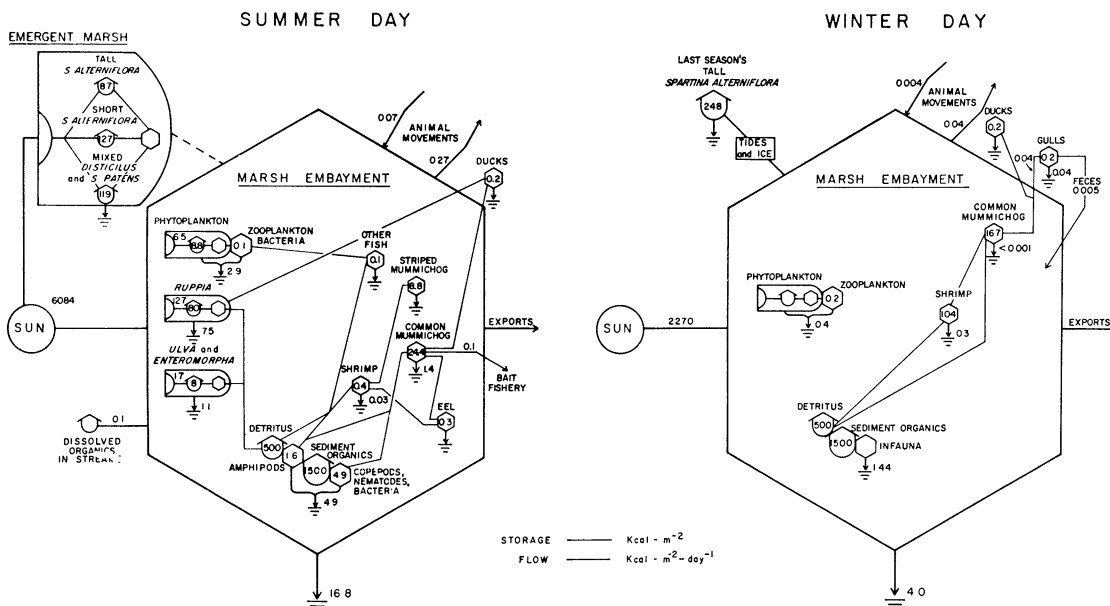
FIG. 23. Energy-flow diagrams for composite winter and summer days in the Bissel Cove marsh. Values were calculated with biomass estimates from the study, the heat of combustion measurements in Table 16, and an oxycalorific constant of 4 Kcal gm^{-1} O$_2$ (Odum 1971). Symbols follow Odum (1967, 1971, 1972).

may result over short periods from submerged vascular plants, attached algae, and phytoplankton in the embayment. When metabolism, population sizes, and migration (Fig. 10, 17, and 19) are analyzed for the whole year, however, the marsh embayment emerges as a consumer system that must depend on the import of organic matter fixed on the emergent marsh by grasses and sediment algae. This result placed the marsh embayment with other systems, such as some highly polluted marine bays (Odum et al. 1963) and woodland streams with leaf litter (Hall 1970), where large inputs of organic matter are received and respiration exceeds photosynthesis.

An ecological energy budget for the marsh embayment over an annual cycle is given in Table 15.* The excess of consumption over production of about 1.4 × 10^6 Kcal yr^{-1} indicates that the embayment must depend on organic inputs to supplement production within the system. A possible second alternative, in which the system could be metabolizing past organic storages, is unlikely in an environment where low oxygen may limit respiration and organic matter is accumulating in the sediments. The value used for total organic input to the embayment is largely a function of the estimate of detritus entering from the emergent marsh. Measurements of the ice-shear zone in the Bissel Cove marsh indicated that only the fringing band of tall or creek-bank *Spartina* was carried into the water, at least as large pieces of grass. The budget in Table 15 has been calcu-

lated assuming an available grass input equal to the production of tall *S. alterniflora* only (Table 1), or 23% of the total emergent grass production. Estimates by Teal (1962) suggest that as much as 45% of the grass may be exported to the estuary via the tidal creeks and embayments. If this value is used, the excess organic matter available for storage in the embayment and export to the estuary would increase to 470 Kcal m^{-2} yr^{-1}, or 4.3 × 10^6 Kcal yr^{-1} from the entire area. The excess consumption of material in the embayment system amounted to about 14% of the total emergent marsh produc-

TABLE 15. Annual energy budget for the Bissel Cove marsh embayment

Item	Kcal m^{-2} yr^{-1}	Kcal yr^{-1}
Production of organic matter within the embayment[a]	9.6 × 10^3	63.4 × 10^6
Consumption of organic matter within the embayment[a]	9.8 × 10^3	64.8 × 10^6
Excess of consumption over production	2.0 × 10^2	1.4 × 10^6
Imports of organic matter from streams[a]	15	1.0 × 10^5
from net immigration of fish and shrimp[b]	3.5	2.3 × 10^4
from emergent marsh[c]	2.4 × 10^2	1.6 × 10^6
Total imports	2.6 × 10^2	1.7 × 10^6
Excess organic matter available for storage and export	60	3.0 × 10^5

[a] Oxycalorific equivalent of 4 Kcal g^{-1}.
[b] From migration data and calorimetry (3 Kcal g^{-1} for shrimp and 5 Kcal g^{-1} for fish).
[c] Assuming input from 1-m-wide band of tall grass around the perimeter plus total area of the islands and 3.3 Kcal g^{-1} (Udell et al. 1969).

tion, so that the effective transport to the estuary amounted to between 10% and 30% of the grass production, depending on which of the two estimates is used.

The exact relationships between emergent marshes and the interconnecting networks of tidal creeks and embayments will vary with flushing behavior, the shoreline development of the marsh, and a number of climatic and locational factors. The results from Bissel Cove indicate, however, that even in the less extensive marshes of New England, the development of large populations of fish and shrimp in the marsh area can be documented, and that the maintenance of the system necessary for the culture of these large popualtions depends on inputs of organic matter from the productive meadows of *Spartina*.

A SIMULATION MODEL OF DIURNAL DISSOLVED OXYGEN[2]

The seasonal summaries, flow diagrams, and annual budgets given in Fig. 10, 16, 18, and 22 and in Tables 1 and 15 help to synthesize many measurements of the diverse parts of the Bissel Cove marsh. It is more difficult, however, to give an impression of the ways in which these parts combine dynamically through time to produce characteristic patterns for the whole system; or, further, to determine if measurements of any one part are reasonable within the context of the larger system. In other studies, where the community of the emergent marsh was emphasized, this problem has led to the development of a compartment model for *Juncus* production in North Carolina (Williams and Murdoch 1972) and to a simulation of phosphorus flux in Georgia (Pomeroy et al. 1972). For Bissel Cove, where most of our effort was directed toward the marsh embayment, it was possible to incorporate biomass and metabolism measurements of dominant parts of the community into a mathematical model to simulate dissolved oxygen levels in the water.

Dissolved oxygen models

Dissolved oxygen has often been modeled with great success by sanitary engineers in water-quality studies of rivers and streams, but their efforts have usually been extensions of the basic oxygen-sag equation developed by Streeter and Phelps (1925). This approach can only be successful in situations approaching a steady state over short time intervals, and where the primary determining factors in the oxygen balance are high BOD loads, temperature, flow rates, and re-aeration. Although recent at-

tempts have been made to include photosynthesis and respiration terms in the equations (see discussion by O'Connell and Thomas 1965, Camp 1965 and Thomann 1971), most water-quality models either ignore the terms in actual computations or use very simple constants to add or subtract oxygen. The calculations in these models are also necessarily put on a long-time base to give a "representative" oxygen value each day or week, since the models do not realistically handle short-term variations. This approach may produce acceptable predicted values in some cases, but it is not applicable to the marsh embayment or other waters where the biological system dominates the oxygen pattern and diurnal changes may be greater than average differences in seasonal values. The only short-term simulation model of dissolved oxygen that appears to have been developed is a charge-discharge compartment model of laboratory blue-green mats by Sollins (1970) that includes light and temperature effects on photosynthesis and respiration.

The Bissel Cove model

Equations were developed relating the oxygen production and consumption by the major compartments of the embayment community to temperature and light energy. These were based on regression of laboratory data of individual metabolism and field biomass measurements discussed earlier (Fig. 11, 15, 16, and 17). For two of these compartments, gross production of sediment microflora and detritus respiration, it was necessary to use literature values (Odum and de la Cruz 1967, Pamatmat 1968). Since this was a diurnal model of oxygen flux, rather than a long-term growth model, the size of each compartment was input for each simulation day and held constant through that run. Simulations were made for 24-hr periods that coincided with each of the 17 days on which diurnal oxygen levels had been measured as part of the procedure to determine total system metabolism (Fig. 5, 6, 10). Compartment sizes, water temperatures, light values, and an initial oxygen concentration were taken from field measurements for the appropriate day. Calculations of flux due to diffusion used a measured diffusion constant of 0.1 hr^{-1}, with the saturation deficit defined as $SD = 1 - OX/OS$, where OX is the calculated instantaneous oxygen concentration, and OS is the saturation value for oxygen at each temperature and salinity calculated from an empirical regression developed by Truesdale, Bowning, and Lowden (1955). The advective contribution of tidal exchange was calculated as the product of flow and duration (tidal volume) times concentration, assuming saturation of incoming bay water. A function generator was used to approximate the

TABLE 16. Components of the Bissel Cove dissolved oxygen model—(H) hourly; (D) daily

Physical inputs	Biological inputs	Outputs
Solar radiation (H)	*Ruppia* biomass (D)	*Ruppia* metabolism (H)
Water temperature (H)	*Ulva* biomass (D)	*Ulva* metabolism (H)
Salinity (H)	Detritus biomass (D)	Detritus respiration (H)
Diffusion constant (D)	Shrimp biomass (D)	Shrimp respiration (H)
Depth ((H)	Fish biomass (D)	Fish respiration (H)
Tide height, duration (H)	BOD (H)	Plankton metabolism (H)
Initial O_2 concentration (D)		Sediment metabolism (H)
		Dissolved O_2 (H)

shape of the tide in the embayment as given by the recording tide gauge (Fig. 4).

The simulation program was written in G-level FORTRAN IV and processed by an IBM 360-50 computer. Numerical integration using Simpson's rule provided the predictions of dissolved oxygen at ⅛₄-hr intervals throughout each 24-hr simulation run. A list of the equations used is included below. Units are g O_2 m^{-2} hr^{-1} unless otherwise defined.
Plankton gross production (Fig. 11):

$$PGP = 10^{(0.0138 \times SR - 1.655)}$$

where SR = solar radiation in cal cm^{-2} hr^{-1}.
Plankton respiration (Fig. 11):
$$PR = 10^{(0.058 \times TW - 2.74)}$$

where TW = water temperature in °C.
Benthic microflora gross production (Pamatmat 1968):
$$BMP = 1.79 \times 10^{-3} \times SR$$
$$+ 4.51 \times 10^{-3} \times TW - 0.0223.$$
Sediment community respiration (see text):
$$SDR = 1.57 \times 10^{-3} \times TW + 9.71 \times 10^{-3}.$$
Ulva respiration (Fig. 15):
$$UR = U(0.101 \times TW - 0.345).$$
Ulva gross production (Fig. 15):
$$UGP = UR + UAP(U)$$

where U = biomass of *Ulva* in mg m^{-2} and UAP = function generator based on Fig. 15.
Ruppia respiration (Fig. 15):
$$RR = R(0.172 \times TW - 1.34).$$
Ruppia gross production (Fig. 15):
$$RGP = RR + RAP(R)$$

where R = biomass of *Ruppia* in mg m^{-2} and RAP = function generator based on Fig. 15.
Detritus respiration (Odum and de la Cruz 1967):
$$DR = D(0.0259 \times TW + 0.097)$$

where D = biomass of detritus in mg m^{-2}.
Shrimp respiration (Fig. 16):
$$SR = S(0.123 \times TW + 0.917)$$

where S = biomass of shrimp in mg m^{-2}.
Fish respiration (Fig. 16):
$$FR = F(0.12 \times TW + 0.42)$$

where F = biomass of fish in mg m^{-2}.

With the above terms combined in an oxygen balance, the final equations for calculating changes in dissolved oxygen in the water appeared as follows:

$$O_2 = PGP + BMP + UGP + RGP - PR - SDR$$
$$- UR - RR - DR - SR - FR \pm \text{diffusion}$$
$$\pm \text{tidal flux}$$

$$O_2 = \int (\dot{O}_2).$$

A summary of the components of the complete model is given in Table 16.

As with all such efforts, the amount of data available and the need for simplification placed limits on the embayment model. For example, while the correlation coefficients for the individual regressions (see individual sections) indicated that temperature and light were the dominant factors influencing metabolism in the embayment, neither the measurements nor the model included other factors such as salinity, nutrient levels, oxygen tension, or seasonal and daily behavioral rhythms that may have influenced metabolism. Since detailed measurements of benthic plant biomass were only taken during summer, when the plants were most abundant, the less reliable field estimates of coverage and relative abundance were combined with the detailed results of an earlier study of nearby Great Pond, Falmouth, Mass., by Conover (1958) to pro-rate values throughout the year. The metabolism of both the plankton and the sediment compartments was related to volume and area, respectively, rather than to numbers or biomass of any particular species. Although this is a common practice in ecological research, a substantial amount of detail has been missed. The error is probably greatest for plankton ($r = 0.65$), since the respiration of sediments appears to be due more to a ubiquitous and rich microbral flora rather than to larger infauna species that may fluctuate widely in numbers (Fenchel 1969). The respiration of less abundant animals, such as the eel and the blue crab, was not included in the model since preliminary calculations showed that their contribution to the diurnal oxygen budget was insignificant, even during their most conspicuous periods. With these limitations in mind, however, the model did serve as a useful method for resynthesizing measurements of individual parts to see if they were reasonable when combined and compared with independent measurements of the whole system.
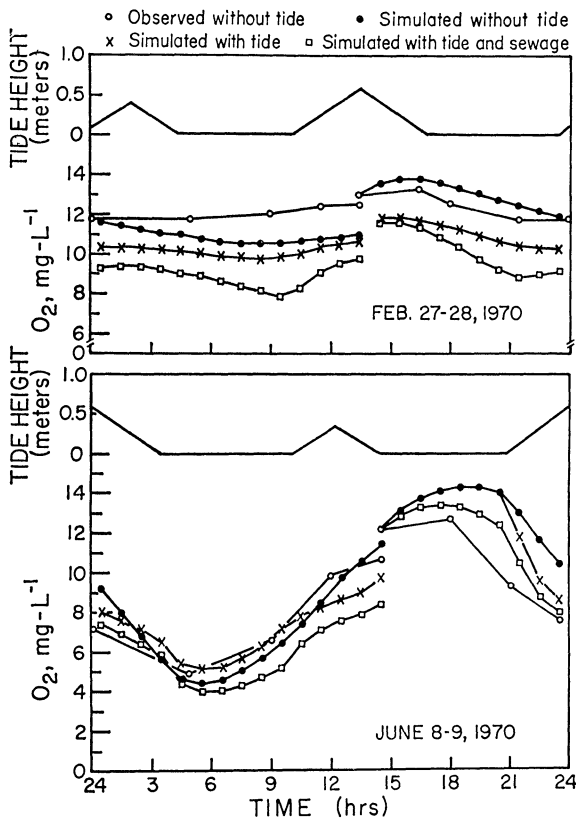
FIG. 24. Comparison of simulated and observed concentrations of dissolved oxygen in the marsh embayment for representative winter and summer days without tidal exchange. The effects of appropriate tidal and sewage BOD inputs have also been simulated.

Simulation and verification

The model produced appropriate patterns and magnitudes of dissolved oxygen for each of the 17 days on which observed diurnal curves were available. Correlation coefficients between observed and simulated curves for each season are shown in Table 17, along with the correlation between observed data and two arbitrary reference functions, a straight line and a sine wave. The high values for the sine

TABLE 17. Correlation coefficients between observed and simulated oxygen values, between observed values and a straight line[a], and between observed values and a fitted sine wave[b]

| | Observed vs. simulated | Observed vs. straight line | Observed vs. sine wave |
Date			
February 27–28	0.59	0.44	0.86
May 12–13	0.93	0.51	0.97
June 8–9	0.83	0.39	0.92
October 8–9	0.81	0.42	0.93
July 8–9 (with tide)	0.98	.24	0.93

[a] Fit by the method of least squares.
[b] The sine wave for each day was fit by matching its period, amplitude, and time of maximum to the observed data.
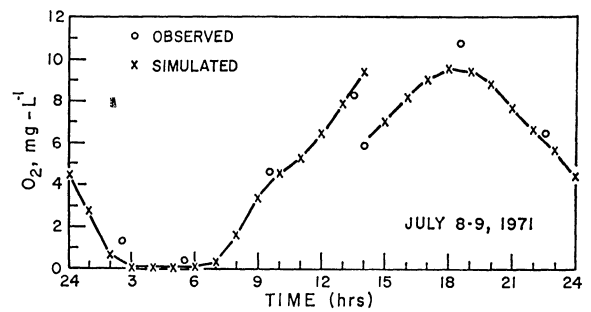

FIG. 25. Comparison of simulated and observed concentrations of dissolved oxygen in the marsh embayment when open to tidal exchanges.

function reflect the symmetry of the diurnal rate-of-change curves for this system, in which a slightly greater night respiration was closely coupled to apparent production during the day (Fig. 9). Representative diurnal curves with simulated and observed values are shown in Fig. 24 for winter and summer extremes, and in Fig. 25 for a day in July when the embayment was open to the tide.

Analysis of the simulation results indicated that phytoplankton contributed about 50% of total system production in the embayment model during winter, with about 40% from sediment microflora and 10% from macrophytes. The contributions of sediment algae remained at 30–40% throughout the year, while the importance of macrophytes increased to a peak of 55% in fall, as the phytoplankton contribution declined to 10%. Respiration results for the model system compartments were as shown in Fig. 10. Respiration by macrophytes, not shown separately, was lowest in winter with 1–2% of total oxygen consumption, then rose to 10–20% of the total during summer and fall. The relative importance of 10 major compartments in the model for a day in June is shown in Table 18. The ratio of total apparent production during the day to the night respiration of the model system has been calculated for each parameter level to give a measure of the

TABLE 18. Response of the Bissel Cove oxygen model to changes in parameter values as indicated by the ratio of apparent production to night respiration (June 8–9, observed $P/R = 0.86$)

Test parameter (X)	Magnitude of parameter change						
	0.0X	0.5X	0.9X	1.0X	1.1X	1.5X	2.0X
Fish biomass	0.92	0.91	0.91	0.91	0.90	0.90	0.89
Shrimp biomass	0.95	0.93	0.91	0.91	0.90	0.88	0.86
Plankton respiration	1.32	1.10	0.94	0.91	0.87	0.73	0.59
Microbenthos respiration	1.34	1.10	0.94	0.91	0.87	0.74	0.60
Plankton production	0.42	0.65	0.86	0.91	0.96	1.17	1.43
Macrophyte biomass	0.27	0.57	0.84	0.91	0.97	1.20	1.43
Macrophyte respiration	1.70	1.25	0.97	0.91	0.85	0.64	0.41
Microbenthos respiration	0.20	0.50	0.82	0.91	0.99	1.33	1.76
Macrophyte production	0.0	0.37	0.78	0.91	1.03	1.54	2.17
Detritus biomass	2.87	1.62	1.02	0.91	0.80	0.48	0.02

relative sensitivity of the model to the magnitude of each compartment or flow. The center column with a *P*-to-*R* ratio of 0.91 resulted from the field and laboratory data as input, and closely approximates the observed ratio of 0.86 for that day.

Effect of the tide

Since small shallow embayments are often subjected to diking and filling operations that decrease or eliminate their exchange with the open estuary, the impact of tidal flows on diurnal oxygen patterns was explored with the model. Simulation runs were made with and without tidal inputs and with the phase moved through the 24-hr cycle. These trials indicated that tidal oxygen effects vary widely, depending on the timing of highs and lows. Results for a typical summer day are shown in Fig. 26 for a tidal excursion in agreement with the maximum observed in the cove. When high tides were simulated at noon and midnight, they had little effect on the oxygen pattern resulting from metabolism of the embayment. When the tides were shifted to morning and evening, however, large changes resulted that increased the diurnal oxygen range and produced almost anoxic conditions at dawn. Instead of damping cycles in the small storage of embayment water as one might first expect, the addition of water from the relatively constant oxygen reservoir in the bay may exaggerate diurnal oscillations. Since dissolved oxygen levels in the bay do not rise as high as those in the embayment, the addition of bay water at the end of the day may sharply lower the concentration of oxygen in the embayment. When imposed on these relatively low end-of-the-day oxygen concentrations produced by the tide, high rates of dark respiration may drive the levels in the marsh to zero during the night. The anoxic production of H_2S occasionally associated unfavorably with shallow coves and marsh embayments may result as much from tidal rhythms as from imports of organic matter injected into an otherwise balanced metabolism.

Simulation of sewage input

Although the Bissel Cove embayment did not have houses built directly by it, marsh waters are frequently used as receiving basins for domestic sewage from surrounding coastal housing. Accordingly, the model was used to determine the effect of sewage additions to the background metabolism of the embayment. On the basis of nearby housing patterns, about 30 houses containing an average of four people each might reasonably be developed in the area. With a typical BOD load of 77.2 g per person per day (C.P. Poon, University of Rhode Island Department of Environmental Engineering,
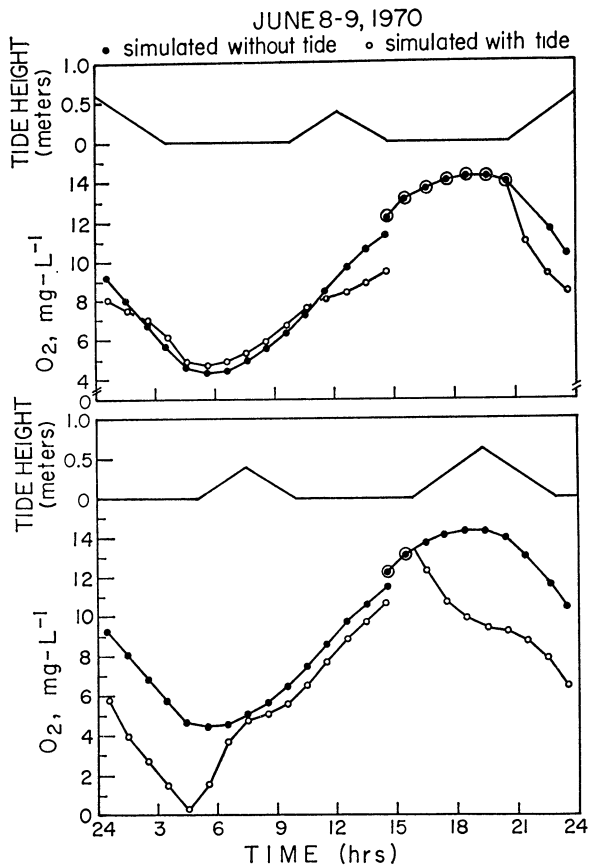
FIG. 26. Simulated effects of different times of high tide on the diurnal oxygen pattern in the marsh embayment on a summer day.

personal communication) the total input to the embayment would be on the order of 9.2 kg BOD day^{-1}. A step function was used to distribute this input so that 25% of the daily total was added between 0800 and 1200, 25% between 1600 and 2000, and the remaining 50% evenly throughout the remaining hours (Poon, personal communication). The model assumed a steady state for sewage and neglected probable effects of nutrients from the sewage in increasing algal biomass or photosynthetic rates. Results of the BOD addition on a winter and summer day with appropriate tide conditions are shown in Fig. 24. The general effect at this level of addition was a reduction in dissolved oxygen of about 1 mg l^{-1} with somewhat greater depressions at times of peak load. When the high tides came at dawn and dusk, however, the additional oxygen demand would produce anoxic conditions in the marsh for several hours.

Simulated temperature increases

The proposed construction of an electric power generating plant nearby on Narragansett Bay

FIG. 27. Simulated effects of water temperature increases on the diurnal dissolved patterns of the marsh embayment.

prompted the simulation of an additional environmental modification, the imposition of thermal loads on the metabolism of the system. The model was run for 1 day each month throughout the year with temperature increases in the embayment for tidal water of 3° C and 10° C. Results for the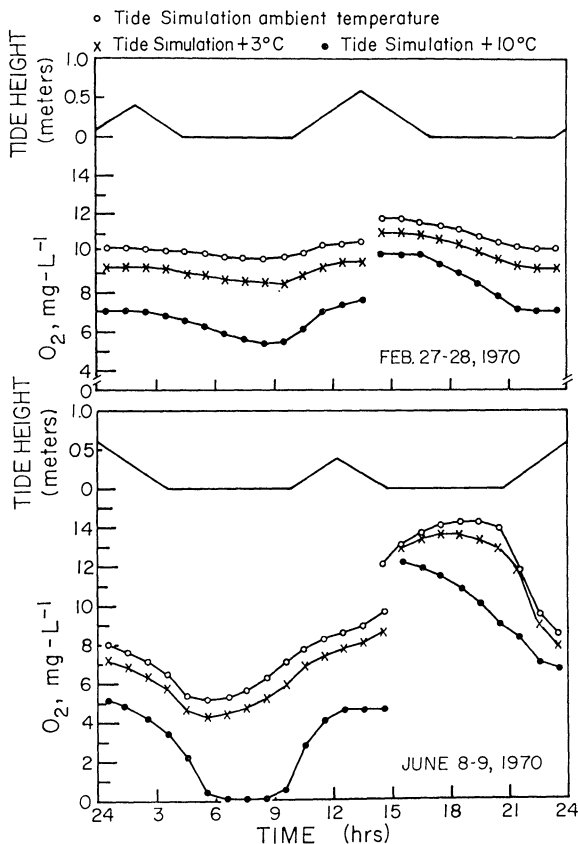 winter and summer days are shown in Fig. 27. An increase of 3° C depressed the oxygen level somewhat less than the addition of 9.2 kg BOD, but a 10° C increase had a marked effect, driving the embayment anaerobic for four or five early morning hours in the summer. Subtle questions of long-term thermal influences on physiology and behavior remain to be answered, but the model is useful in showing that the more realistic small temperature increases that may be associated with thermal shadows from power plant cooling systems may be expected to produce measurable, but slight, lowerings of dissolved oxygen levels in coastal embayments like Bissel Cove.

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