Simulating Spatial and Temporal Fluctuations of Dissolved Oxygen in Flax Pond, New York

by

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Introduction:

G. Evelyn Hutchinson noted that a combination of accurate oxygen measurements with a few physical measurements can provide a great deal of information about the biotic dynamics of a lake (Hutchinson, 1957). We believe this statement to be accurate for lacustrine and riverine systems, but complex processes in tidally influenced waters make the determination of biologically mediated oxygen changes much more difficult. The concentration of oxygen in a temperate salt pond is a function of both the biotic activity of the system and the delivery oxygen-saturated water via tides twice daily. Thus, determining the contribution of biological oxygen rates of change to the total rate of oxygen change in tidally-influenced systems can be quite difficult. For example, in Flax Pond, a salt pond on the northern shore of Long Island, New York, a suite of benthic and free-water flora and fauna photosynthesize and respire at different rates and magnitudes, based upon the hour of the day, day of the year, and location within the marsh (Woodwell *et al*. 1979). A detailed series of chemical, physical, and biological measurements were made in Flax Pond in early 1970's, which makes the pond an excellent location to attempt the distinction between biological and tidal contributions to oxygen dynamics.

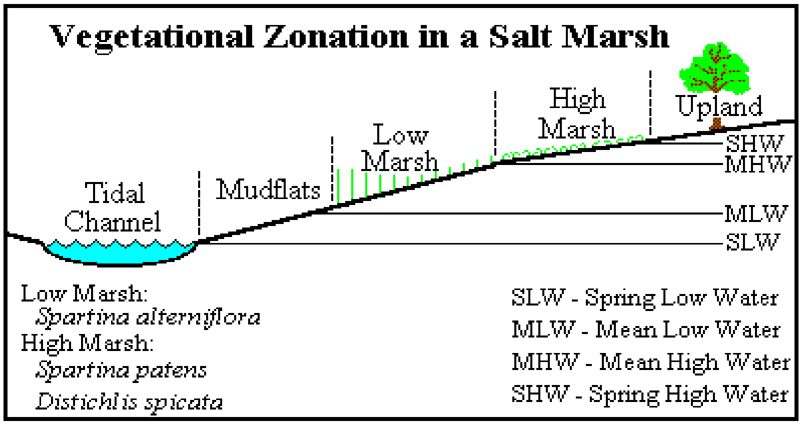
***Study Site*: Flax pond**

Flax pond is a 57 hectare *Spartina alterniflora* marsh on the northern shore of Suffolk County, Long Island, New York (Figure 1 a,b). Roughly 26 hectares of the marsh are *Spartina alterniflora* marsh, 4 hectares are *Spartina patens* and *Distichlis spicata* marsh, and the remaining 27 hectares are tidal creeks and bare sediment (Woodwell *et al*. 1979). The drainage area of the march is roughly 3 times its size, at 168 hectares (Woodwell and Pecan 1973) and is characterized by sandy soils. The pond is connected to Long Island Sound by a single inlet and does not have a fresh or salt water stream moving through it. The pond experiences a daily tidal variation of ~ 2 m and is ~0.5 m deep on average (Hall *et al.* 1979). As a result of gravel mining in the mid 20th century, a large pool (8-14 m deep) is located near the outlet to Long Island Sound (Woodwell and Pecan 1973). The marsh is flushed twice daily by the tide and nearly 80% of the water in the marsh at high tide is removed during tidal fluxes (Woodwell *et al*. 1979). A detailed discussion of the Flax pond marsh is provided in Woodwell and Pecan (1973).

Vegetation type and distribution:

As mentioned previously, Flax Pond is a *Spartina*-dominated marsh, but an assortment of plant species is found there. The salt marsh grass *Spartina alterniflora* is the dominant *Spartina* found in the marsh and is most abundant along the creek banks of the marsh where salinity is lower than inland (Figure 2).

Figure 2: Schematic representation of vegetation zoning in a salt marsh (vertical scale exaggerated)



Replacing *S. alterniflora* in more inland regions of the marsh is salt meadow grass (*Spartina patens*), which is commonly associated with spike-grass (*Distichlis spicata*), marsh elder (*Iva frutescens*), and blackgrass (*Juncus gerardi*) (Heusser and Heusser 1975, Woodwell and Pecan 1973). This community structure is similar to the generalized assemblages described in Conrad (1935) for a Long Island salt marsh, but the community has only been established recently. Flax Pond was once a freshwater or oligohaline pond just inland from Long Island Sound, as peat deposits including *Sphagnum, Ruppia,* and *Typha latifolia* were discovered in cores of Flax Pond sediments (Heusser and Heusser 1975). Local historical records indicate that a channel was dug connecting the pond to Long Island Sound in the late 19th century, in hopes to develop shellfish habitat in the marsh (Woodwell and Pecan 1973). This channel was further dredged in the 1930's to maintain a substantial exchange of water with Long Island Sound. The current state of the pond appears to be unchanged since the depression-era dredging.

Flax pond is a salt marsh/pond that is characterized by brackish water (~26 ppt), a daily tidal cycle with two high tides, and a high biomass of *Spartina alterniflora*. The marsh is similar to many estuarine systems in that it is heavily influenced by the entrance and exit of tide water from the nearby ocean. The inflow of tide waters serves as an energy subsidy to the pond by delivering particulate carbon and dissolved oxygen and by removing toxic metabolic products, such as ammonia, produced during periods of low dissolved oxygen (Day *et al*. 1989). Tidal action also acts as a stress, as regions of the marsh are exposed to the atmosphere for part of the day and inundated with water later on. The physical stress of tidal currents on plant and animal life also has potentially negative impacts on organisms inhabiting the marsh. For these reasons, salt marshes and estuaries are generally not very diverse, but are highly productive. For example, the individual, above ground net primary productivity of several plants (e.g. *Distichlis* *spicata*, *Juncus roemerianus*, *Spartina alterniflora*, *Spartina patens*) in Louisiana salt marshes ranges from 1,162-4,159 tons dry matter ha^{-1} yr^{-1} (White *et al*. 1978, Hopkinson *et al*. 1980). Those organisms that manage to adapt to the stressful conditions have a bounty of nutritional material to utilize in the estuarine sediments and, to a lesser extent, the water. Estuaries are also important nurseries for many recreationally and commercially important fish species (Day *et al*. 1989). This also appears to be the case in Flax Pond, as high fish biomass (average 80 g m^{-2} wet weight) is recorded in the marsh during late summer and fall and juvenile fish are the predominant fish found in the pond. For these reasons, estuaries like Flax Pond are considered to be biological systems with an importance far greater than their size would suggest.

Although dissolved oxygen has historically been modeled for streams and rivers (Streeter and Phelps 1925, Odum 1955) and marine benthic systems (Borsuk *et al*. 2001), few models have been generated to predict oxygen concentration as a product of net ecosystem metabolism (i.e. the summation of the metabolism of all biotic compartments within a system). Nixon and Oviatt (1973) achieved reasonably accurate predictions of short-term changes in dissolved oxygen concentration in Bissel Cove, Narragansett Bay, RI, using an ecosystem metabolism approach. Although this model included predictions of the concentration of oxygen in the cove, it did not included a spatial assessment of dissolved oxygen changes over time. Such a spatial pattern of oxygen variation can be important because dissolved oxygen concentrations often vary over short, 6-meter distances in systems like Flax Pond (C. Hall, unpublished observations) and very large variations in oxygen can exist over large distances. These small-scale spatial differences result when water is left in flooded pools following tidal retreat or unequivocally to variations in the surface to volume ratio in different parts of the pond where benthic metabolism is intense (e.g. tidal creek, deep pool, *Spartina* marsh). A good model of the spatial variations of dissolved oxygen changes in Flax Pond therefore will allow us to predict the concentration of dissolved oxygen in all parts of the pond through diel, daily, and yearly intervals.

With Flax pond, we are provided with an ideal setting to measure exchanges with Long Island sound and to construct a simulation model. The only freshwater that enters Flax Pond comes in the form of precipitation, groundwater seepage, and surface/subsurface runoff (Woodwell and Pecan 1973). The magnitude of these fluxes is considered to be fairly small (Moll 1977, Woodwell *et al*. 1979), as a 2-year study revealed a salinity variation of <1 ppt within the pond (Woodwell *et al*. 1977). With little freshwater input, salinity in consistent throughout the pond and primary production is not affected by large amounts of terrestrially derived nutrients entering the pond *via* groundwater (Johannes 1980). Most coastal salt marshes are influenced by the passage of a stream or river through the marsh on its way to the ocean. River water interacting with the incoming tide water creates a complex situation in respect to water mixing, flow rates, and salinity. In Flax Pond, these phenomena are not present and we can simply simulate water flow into and out of the pond, while assuming constant salinity. In addition, Flax pond was the site of an intense investigation by Brookhaven National Laboratory from 1971-1974. This study explored many components of the Flax Pond Ecosystem, including the exchanges of nutrients between Flax Pond and Long Island Sound, the sedimentation rates within the marsh, the marsh carbon budget, and oxygen fluctuations within the pond (Armentano and Woodwell 1975, Whitney *et al*. 1975, Woodwell *et al.*

1975, Hall *et al*. 1979). Extensive records of dissolved oxygen concentration were maintained at the mouth and at an interior “bridge” site of Flax Pond.

The model presented in this report is an attempt to simulate the variation in dissolved oxygen concentration in Flax Pond over space and time, based tidal dynamics, pond morphology, and an extensive biological database. We do not predict changes in biomass due to grazing, herbivory, or any trophic transfer, but rather we have simulated the contribution of each biological component to prevailing dissolved oxygen concentrations, based on measured values. In employing this type of method, temperature, sunlight, and time of day/year are the only forcing functions in the system. Our objective is to validate our simulated oxygen values with measurements taken at the mouth of Flax Pond and in the marsh interior. We propose to do this in the following manner: simulate the movement of water into Flax Pond at measured values for an incoming tide; to incubate the water in the pond by exposing it to the oxygen consuming/producing activities of the biotic compartments of the pond; and to validate the incubated water as it leaves the pond with measured values of oxygen for the outgoing tide. We will use these validations to investigate whether our assumptions about the oxygen dynamics of Flax Pond are accurate.

Methods:

We have simulated the photosynthetic and/or respiratory activities of fish, *Spartina alterniflora*, fucoid algae, phytoplankton, and benthic communities in Flax Pond at a time interval of 15 minutes for each day of 1 year. The sum of these biological oxygen consuming/producing activities was coupled to the movement of tidal water through Flax Pond to yield a concentration of oxygen (g m^{-3}) in a 6m x 6m cell spatial image every 15 minutes.

Data Collection*:*

Tidal Water Samples:

The data available for parameterization of our simulations were measured between 1971 and 1974 in Flax Pond. The studies were carried out at Brookhaven National Laboratory. Our basic chemistry data set was based on eight water samples collected once a week over a single tide cycle (see Woodwell *et al.* 1977). Four of these samples were collected at equal intervals during an incoming tide and four at equal intervals on an outgoing tide. The water moving through tidal channels was turbulent and shallow enough so that thorough mixing could be assumed (Woodwell *et al*. 1979). Chlorophyll *a*, dissolved oxygen, and various dissolved nutrients were measured in water samples, while water temperature and tide depth were also recorded. Dissolved oxygen and temperature were also measured somewhat regularly below a bridge at the interior of Flax Pond for 24 hour periods.

Benthic oxygen:

Total benthic metabolism was measured *in situ* using benthic chambers (Hall *et al*. 1979) (see Figure 3). Benthic chamber measurements were made for 24-hour periods bimonthly in 1974. Total benthic metabolism includes the combined photosynthetic and respiratory activity of algae, bacteria and invertebrates enclosed in the plexiglass chamber. The use of these chambers permits the measurement of hourly differences in dissolved oxygen concentration of water incubated in the chamber, which are refreshed once an hour with water from outside the chamber. The difference details the amount of dissolved oxygen produced or consumed within the chamber relative to the "free" water of the marsh. The net metabolism of benthic communities was measured and compared to variations in solar radiation and temperature during 24-hour periods over 8 months. The design of the benthic chambers used in this study included a pump that simulated the current over the marsh bottom.

Simulations:

Simulations were constructed using FORTRAN 90 and then expressed spatially using Idrisi software (Release 2). All biotic compartments contributing to oxygen fluctuations were simulated at 15 minute intervals for each 6 x 6 meter cell in a 158 x 300 cell raster digital elevation model (DEM) (see Figure 1c).

We simulated the metabolic (i.e. oxygen producing/consuming) activity of benthic communities, phytoplankton, *Spartina alterniflora*, submerged marsh algae, and fish as they were progressively subjected to tidal inundation and varying oxygen concentration over a tidal cycle (Figure 4). We also incorporated seasonal and daily patterns of temperature and solar insolation as the energetic drivers of metabolism.

Tidal Simulation:

We simulated tide height (m) every 15 minutes of each day using a modified SINE curve. The simulation was generally based upon data collected by Tempel (1973) in Flax Pond, and included two daily peaks in tide height that correspond to high tide. Due to a sill at the exit of Flax Pond, the tide rose from 4.5 hours and fell for 8 hours. By adding the tide height to the depth of each cell in the DEM, we can predict the volume of water in each cell in the raster-based representation and therefore the total volume of Flax Pond at each time step. The resultant prediction was validated against measurements of total marsh water volume made in 1971-1974 using stereoscopic aerial images. An aerial image of Flax Pond was taken in 1971 during low tide and subsequently used to generate a topographic map with 2 ft contours (Woodwell and Pecan 1973). Surface water area at various contours of the topographic map were multiplied by mean water depth at each tide to generate the volume of the entire pond (Woodwell and Pecan 1973).

```
DO TIDE = 1, 96
        HORIZ           = HORIZON + TIDE
```

```
RADIANS      = HORIZ*RAD
PERIODVAL  = PERIOD*RADIANS
        TIDEDEPTH   = ((SIN(PERIODVAL)+VERT)*AMP)
 END DO
```

Where HORIZ = horizontal shift in SINE curve relative to midnight (shifts 1 hour later each day)
RAD = conversion to radians
PERIODVAL = shift if the SINE curve period
TIDEDEPTH = tide depth (m) relative to low tide depth = 0 m
VERT = vertical shift in normal SINE curve to make all values > 0 m
AMP = manipulation of standard SINE curve amplitude of 1 to 2.3

We simulated a spring tide every 29 days of the year and a neap tide at an even interval between spring tides. High tide was predicted to occur an hour later than the previous day. Both of these simulations were based on tide data from Smithtown Bay, Long Island Sound, New York, which is just southeast of Flax Pond.

Considering that Flax Pond does not include a freshwater stream, we can simplify a simulation of tidewater flow through the pond. As mentioned previously, we simply 'fill up' or 'empty' each cell of the marsh when the tide is rising or falling. This bathtub approach predicts how much water will be in a cell at a given time, but fails to account for the movement of the tidal current and its effect of dissolved oxygen. We have therefore divided the marsh into 9 sections (Figure 4). Waters entering the pond from Long Island Sound are saturated with oxygen and the movement of this saturated water in tidally forced water movement through the pond is responsible for much of the pond's oxygen dynamics. Thus, we simulate the movement of dissolved oxygen through the pond, as we simulate the flow of water.

The primary components of this simulation are listed below:

1. Flax Pond is divided into 9 sections and all cells in the raster representation are assigned to a section

2. All cells are given an initial dissolved oxygen concentration. The initial concentration is based on low tide values in Flax Pond in January
3. The metabolism of each biotic component is simulated at 15-minute intervals for each cell in each section of the raster-representation of Flax Pond.
4. The net metabolism (g O_2 15-min.$^{-1}$) of each cell is added or subtracted from the initial O_2 concentration of each cell for three time steps (i.e. the water incubates in 1 section for 45 minutes)
5. Calculate the average oxygen concentration (g m^{-3}) of all the cells in a given section after 45 minutes
6. After 45 minutes, water with the average O_2 concentration from the past 45 minutes is moved to the next section in a block-like manner (in the direction of water flow). All cells in the newly updated section are initialized for the next time step with the average oxygen concentration from the previous section. (cells in the section at the mouth of the marsh are updated with the calculated oxygen saturation value for the given temperature if the tide is rising)

This simulation, although somewhat crude, provides us with the movement of water and its contained oxygen through Flax Pond that our model requires.

Solar Insolation:

Maximum daily solar radiation was simulated using a COSINE function similar to that used in Nixon and Kremer (1977) and adjusted slightly to match data recorded in Flax Pond in 1974 by Hall *et al.* (1979). Thus, we simulate light with a function that varied the daily and hourly inputs of solar radiation throughout the year.

$$\text{RadMax} = 0.08 * (677.5 - 371.5\ \text{COS}\ (2.14\Pi\ (\text{JDAY} + 10) / 360))$$

Where RadMax = Maximum clear sky radiation (Kcal m^{-2})

JDAY = Julian calendar date (January = 001)

We generated a stochastic cloudiness factor for each day of the year using daily cloud cover data from the National Weather Service from 1998-2002. The National Weather Service data expressed cloud cover in tenths as the fraction of the sky covered by clouds. We used a random number generator in FORTRAN 90 to estimate cloud cover based upon day to day trends presented in the data. Considering that cloud cover is highly variable even with historical data, we simply predicted 90% of the days to be cloudy from January to May, 85% of the days in June, November, and December, and 75% of the days in July through October. These percentages were chosen based on the average number of days that were cloudy in the National Weather Service database. A random number from 0-1 was then generated for each simulated cloudy day. The simulated cloud cover value for each day was then subtracted from the maximum potential radiation for each day using the following equation (Sverdrup *et al*. 1942):

$$IRad = RadMax\ (1.0 - 0.71\ (CloudCov)\ )$$

Where IRad = simulated light incident at sea level with cloudiness (Kcal m^{-2})

CloudCov = cloud cover in tenths

We ran two simulations of sunlight in our Flax Pond model, one with stochastic cloud cover and another with full sunlight.

We simulated hourly solar insolation values using a SINE curve. The maximum radiation for a given day (IRAD) was calculated as the solar insolation at noon, when the sun is highest in the sky.

$$INS1 = Sin(((HR-24)*3.75)*(3.14/180)) * IRAD$$

Where HR = time of day

INS1 = incident solar radiation (Kcal m^{-2} hr^{-1})

Day length fluctuates seasonally at temperate latitudes, as in Flax Pond (41°N, 73°W). To account for the effects of day length on photosynthetic processes, we simulated day length, based on the times of sunrise and sunset at Brookhaven, NY (from National Weather Service data), which is a neighboring town to Flax Pond. Day length varies from ~9 hours per day at the seasonal minimum to ~15 hours per day at the seasonal maximum.

Temperature:

Water temperature varies seasonally and daily in a sinusoidal manner. Thus, we employed a COSINE function to simulate average daily temperature in Flax Pond waters using the following equation:

TEMP = (SIN((JDAY-90)*0.01745329)*9.7)+14.2

Where TEMP = average daily temperature (^{o}C)

We assumed water temperature to be constant throughout the waters of Flax Pond. We then simulated water temperature every 15 minutes by mimicking measured temperature values recorded in the water column by Hall *et al*. (1979). The average daily temperature was used to parameterize this simulation. The temperature of Flax Pond waters peaked twice during the day, once at ~6 am and then a higher peak at ~6 pm.

Oxygen Solubility:

The saturation concentration of oxygen in Flax Pond varies seasonally, primarily in response to water and air temperature. Based on studies of oxygen saturation in marine waters by Truesdale *et al*. (1955), daily and 15 minute solubility vales for dissolved oxygen in Flax Pond were predicted in response to temperature and salinity. Since the salinity of Flax Pond is almost always within <1 ppt of 26 ppt we assumed a salinity of 26 ppt in making solubility calculations.

SatVal = 14.161-(0.3943*TEMP)+0.007714*(TEMP)**2)(0.0000646*(TEMP*3))-
2.1866+ (0.06656*TEMP)- (0.000972*(TEMP)**2))

SatDef = 1 – (SatVal/OxyConc)

Where SatVal = concentration of dissolved oxygen at saturation
SatDef = the deficit below saturation of oxygen in Flax Pond
OxyConc = the concentration of dissolved oxygen in Flax Pond
*(a salinity of 26 ppt is calculated in one of the constants of this equation)

The diffusion of oxygen into and from Flax Pond waters in a function of saturation deficit and diffusion. Therefore, the saturation deficit at a given time is the amount of dissolved oxygen that will diffuse into the water. Although no direct diffusion measurements were available for Flax Pond, see Copeland and Duffer (1964) for a discussion of oxygen diffusion measurements.

Photosynthesis of benthic communities:

The benthic community simulations we made were, as mentioned previously, based on recorded data from Flax Pond. The benthic chambers accounted for the accumulated photosynthesis of benthic communities, including algal, bacterial, and invertebrate metabolism.

Photosynthesis in Flax Pond benthic communities was predicted as a function of incident solar radiation. Gross photosynthesis (g 0_2 m^{-2} 15-min.$^{-1}$) was generated using a Michaelis-Menten function that predicts photosynthesis to saturate at high levels of solar insolation (Figure ??). Using this function, gross photosynthesis reaches an asymptotic maximum despite increases in solar insolation. We again used a SINE curve to simulate gross photosynthesis every 15 minutes, using data measured in Hall *et al*. (1979).

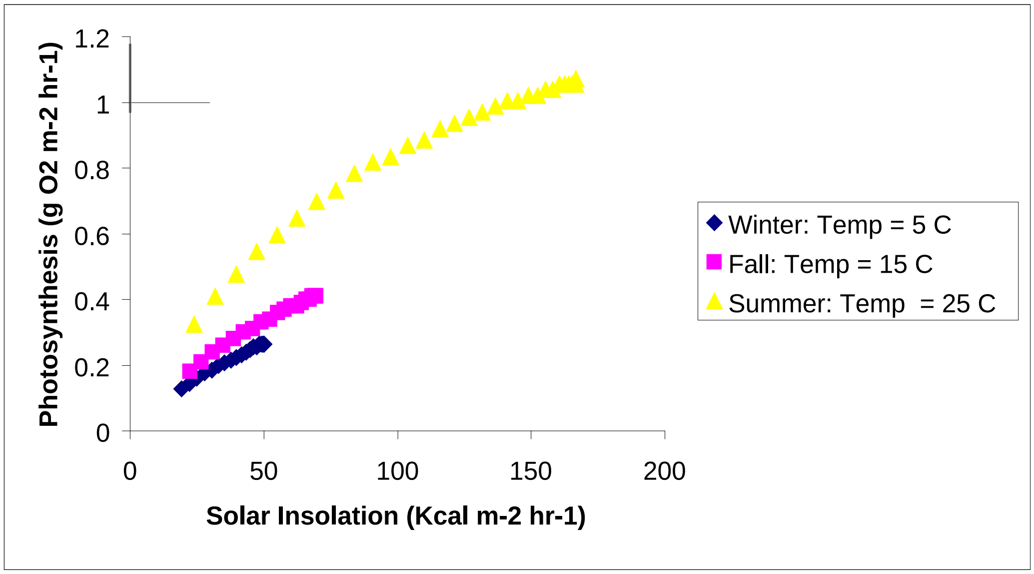
LitLim = INS1/(KS+INS1)

PS = (GMAX * LitLim)

Where LitLim = Michaelis-Menten light limited photosynthesis (g 0_2 m^{-2} 15-min.$^{-1}$)
KS = 10 = Half saturation coefficient
PS = Gross photosynthesis (g 0_2 m^{-2} 15-min.$^{-1}$)
GMAX = asymptotic photosynthetic maximum

We varied the factor *LitLim*, which served as a saturation value for benthic photosynthesis to account for seasonal changes in average temperature (Figure ??).

Figure ??: Variability in seasonal photosynthesis saturation due to temperature differences



This factor was higher during warm months (June-September) and decreased during cold months (November-February). We accomplished this variation by making *LitLim* a function of temperature, which varies seasonally with lowest values in winter and highest in summer. The variation we were seeking ranged between 0 and 2.5, which made a calculation of temperature based *LitLim* much easier. Thus, we simply varied *LitLim* by adding to it the value of daily average temperature multiplied by 0.1. We incorporated this seasonal variation because peak benthic photosynthesis was recorded in the warmer summer months in Flax Pond, not the late spring months, as in other aquatic systems.

Respiration of benthic communities:

We predicted respiration in benthic communities as a function of water temperature. Respiratory processes are assumed to double with every 10^{o}C increase in temperature and we used a Q_{ten} equation to quantify the temperature-respiration relationship.

RESP= 1*Q_{ten}**(TEMP/10)

Where RESP = respiration of Flax Pond benthic communities (g 0_2 m^{-2} 15-min.^{-1})
Q_{ten} = 1.5

Phytoplankton photosynthesis and respiration:

The influence of phytoplankton on the cumulative metabolic activity of Flax Pond is fairly small (Moll 1977). The shallow water of the marsh was found to produce only 11.7 g C m^{-2} of marsh in a year (Moll 1977). Despite the low productivity of plankton, we estimated photosynthesis and respiration of plankton in Flax Pond every 15 minutes. We used equations from Nixon and Oviatt (1973) for Narragansett Bay, RI to represent phytoplankton metabolism. These equations predict plankton respiration as a function of temperature and photosynthesis as a function of incident solar insolation.

RPlank = (10**((0.058*TEMP)-2.74))/4

Pplank = (10**((0.0138*INS)-1.655))/4

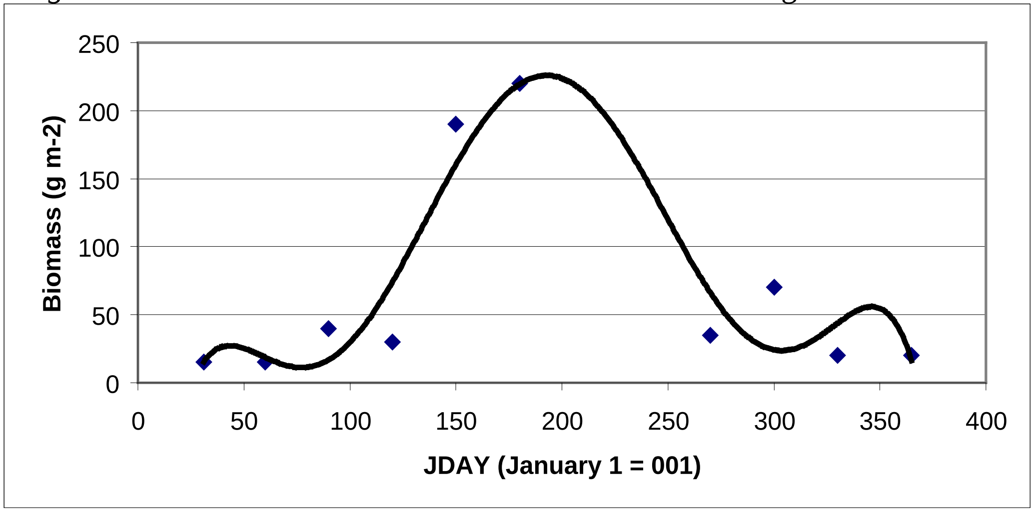
Where Plank = respiration of plankton communities (g 0_2 m^{-2} 15-min.^{-1})
PlankGPP = photosynthesis of plankton communities (g 0_2 m^{-2} 15-min.^{-1})

Each of these equations was based on experimental data in Narragansett Bay, and the values are probably slightly higher than in Flax Pond.

Fucoid algae photosynthesis and respiration:

In addition to *Spartina alterniflora,* the salt marsh flats of Flax Pond are vegetated by the alga, *Ascophyllum nodosum* ecad *scorpiodes*. A series of studies of the seasonal biomass, distribution, and photorespiration of these salt marsh fucoids was carried out in Flax Pond (Brinkhuis 1976, Brinkhuis and Jones 1976, Brinkhuis *et al.* 1976). We have used this data to parameterize a simulation of seasonal biomass (Figure ??) and the daily photorespiration of *A. nodosum* (Figure ??).

Figure ??: Seasonal biomass of *A. nodosum* in intertidal regions of Flax Pond



We added this metabolism to cells located in intertidal regions of the pond system.

FucBioM = (SIN(((JDAY-140)*0.01745329)*1.8)*105.7)+120.2

Where FucBioM = daily biomass of *A. nodosum* in the marsh flats (g C m^{-2})

Photosynthesis and respiration (g C m^{-2} 15-min^{-1}) were estimated every 15 minutes as a function of solar insolation and temperature. The shading of sunlight by *Spartina* stems can reduce algal photosynthesis by 20-50% (Brinkhuis *et al*. 1976). We therefore used a random number to generate a value for photosynthesis as a result of *Spartina* cover.

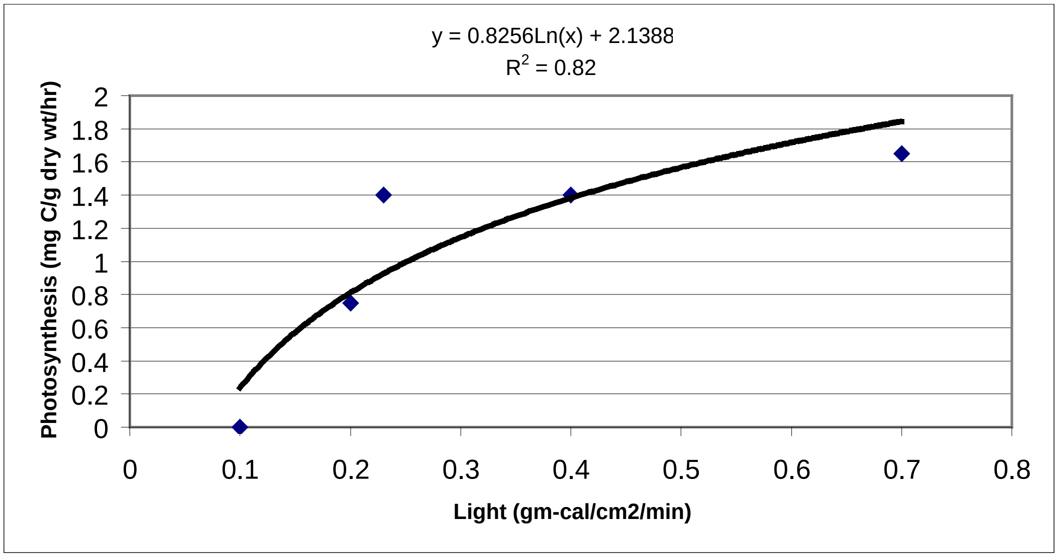
FucPhoto = 0.8256*(LOG(INS*SpartCov)) + 2.1388

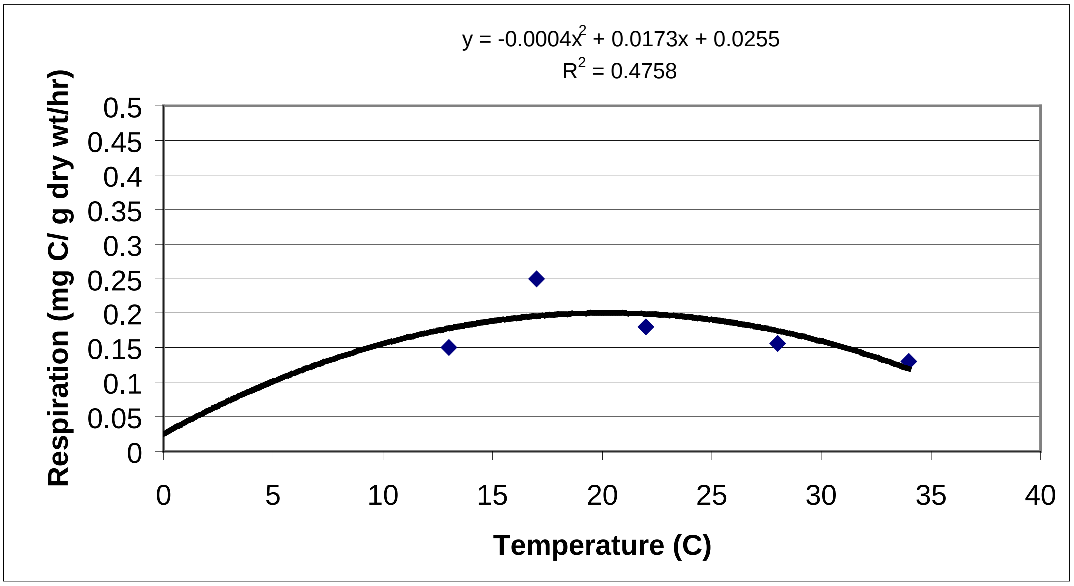
FucResp = -0.0004*(DAYTEMP**2) + 0.0173*DAYTEMP + 0.0255

Where FucPhoto = photosynthesis of *A nodosum* (g C m^{-2} 15-$min.^{-1}$)

FucResp = respiration of *A. nodosum* (g C m^{-2} 15-min.$^{-1}$)
Spartcov = reduction of photosynthesis by *S. alterniflora* stalks

Figure ??: Light dependent photosynthesis and temperature dependent respiration in *A. nodosum*





Simulated carbon values were converted to grams O_2 m^{-2} 15-min^{-1} using a stoichiometric calculation that assumes all fixed carbon is converted to glucose in the general photosynthetic equation:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

$$\text{g C} \div 6 = \text{g } C_6H_{12}O_6 \div 12 = \text{mol } C_6H_{12}O_6 * 6 = \text{mol } O_2 * 32 = \text{g } O_2$$

Although this simplified assumption of photosynthesis and respiration certainly lacks precision, we consider it to be sufficient.

Spartina alterniflora oxygen dynamics:

We simulated the contribution of *Spartina alterniflora* to prevailing dissolved oxygen concentrations during those times when *S. alterniflora* was partially or completely covered by water. We accomplished this using exchange rates of CO_2 with the atmosphere measured by Houghton and Woodwell (1980). We assume all of the vegetated area of the marsh to be composed of *S. alterniflora* in our analysis, as stands of *S. alterniflora* compose 46% of the 54% of the marsh that is vegetated. We therefore consider *S. alterniflora* metabolism to account for most of the upland marsh's exchange of CO_2 with the atmosphere. The measurements made by Houghton and Woodwell (1980) shows that CO_2 exchange with the atmosphere over a single day fluctuates in a sinusoidal manner, with higher variation between minimum and maximum values in the summer and less in winter. The duration of the peaks in CO_2 exchange were also higher in summer than in winter, as the days are longer in summer. Thus, we employed a SINE curve with a seasonally varying amplitude to simulate *S. alterniflora* metabolism.

```
 CO2Amp    = ((SIN((JDAY-110)*0.01745329))*1.5)+1.8
 CO2flux    = SIN((((TIDE-28)*1.17)*3.75)*0.01745329)*CO2AMP(JDAY)
 O2flux       = (CO2flux)/1.38)/4
```

Where CO2Amp = amplitude of SIN curve for daily CO_2 exchange
CO2flux = exchange of CO_2 of water with the atmosphere (g CO_2 m^{-2} hr^{-1}) – negative values indicate net flux of CO2 out of the marsh
O2flux = conversion of exchanged CO2 to O2 (g O_2 m^{-2} 15-min.^{-1})

The conversion of exchanged CO_2 to the equivalent amount of O_2 that would have been consumed/produced *via S. alterniflora* metabolism was borrowed from Hall and Moll (1975). This conversion is a similar simplification as we used in the conversion of grams of carbon produced by fucoid algae to grams of oxygen produced.

$$\text{g } CO_2 \text{ metabolized} / 1.38 = \text{g } O_2 \text{ metabolized}$$

Our simulations of *S. alterniflora* metabolism are much higher than those we have made for benthic communities and phytoplankton. This disparity exists because our simulation estimates the *total* exchange of *S. alterniflora* with the atmosphere and water. Our interests are only in the exchange of *S. alterniflora* with the *water column*. Thus, we calculated the exchange of *S. alterniflora* with the water column by multiplying the total exchange of CO_2 by the height of the water in each cell at each tide. This calculation is based on an assumption that all *S. alterniflora* stalks are 1 meter tall, which is an average of the intermediate growth form of *S. alterniflora* (Blum 1993).

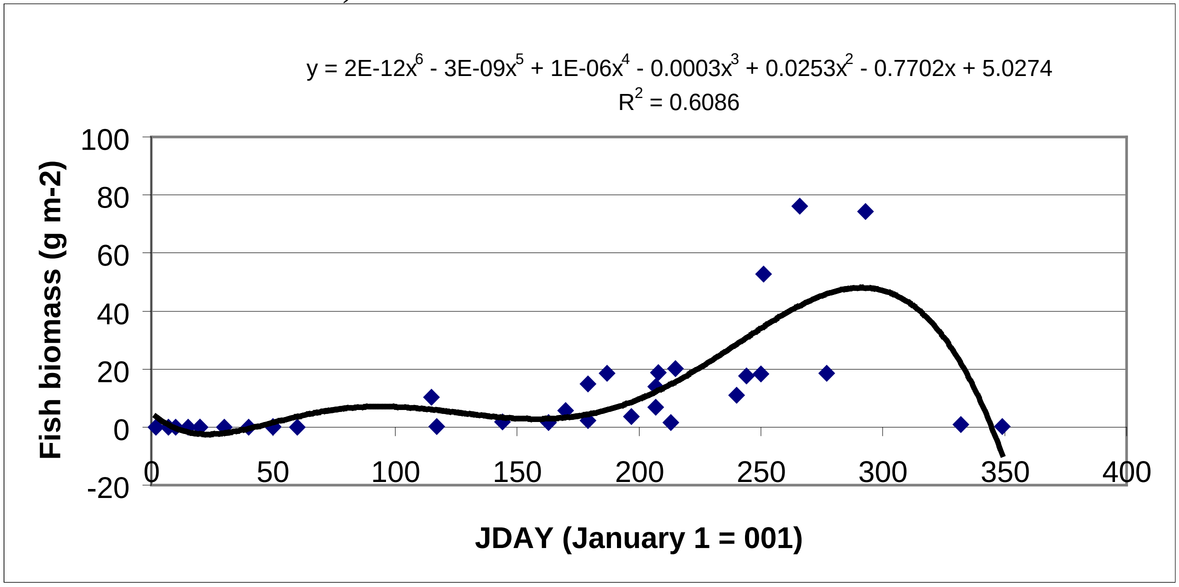
Depth of water in cell / 1 = fraction of S. alterniflora exchanging with water

*Fish metabolism in Flax Pond***:**

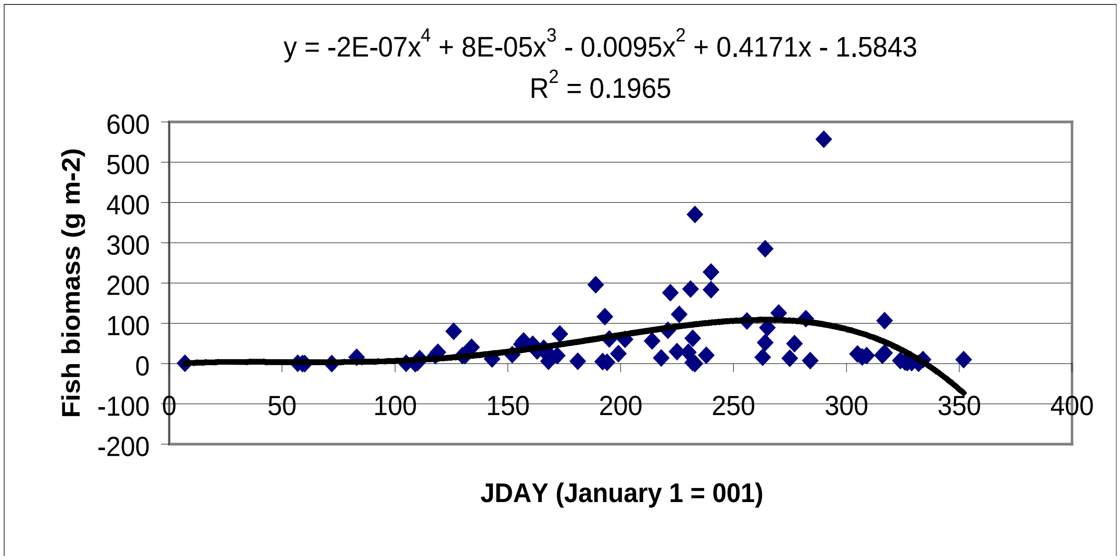
We estimated the contribution of fish respiration to total dissolved oxygen fluctuations, using samples of fish abundance in Flax Pond from 1970-1973. Fish were sampled using a “drop net” seine on various days throughout the year. The seine consisted of a movable, floating frame which supported a 6 m by 7 m net (Figure 5). On sampling days, the seine was moved to the desired location of the pond and left unattended roughly an hour. In doing so, fish were not disturbed immediately prior to sampling. After an hour, the pulling of a trigger dropped the net into the water, effectively trapping all fish contained within it. Samples were taken at low tide only, but we assume the relationship of fish biomass to depth to be linear.

We generated 4 – 6 order polynomial regressions to derive functions of fish biomass (g m^{-2}) for each day of the year in Flax Pond, based on fish samples collected in the early 1970's. The biomass of all fish caught was aggregated into a total fish biomass for each day, instead of analyzing species individually. We assume fish biomass to be constant throughout the diel cycle of a given day of the year. The fish samples were divided into 3 different groups: biomass of fish (g m^{-2}) at depths below 0.5 m, between 0.5 m and 1.8 m, and above 1.8 m. Each regression was used to calculate a fish biomass in each cell of the raster file, based on which depth category the cell fit in at the given tide level. The data and regressions are available in Figure 3 a-c.

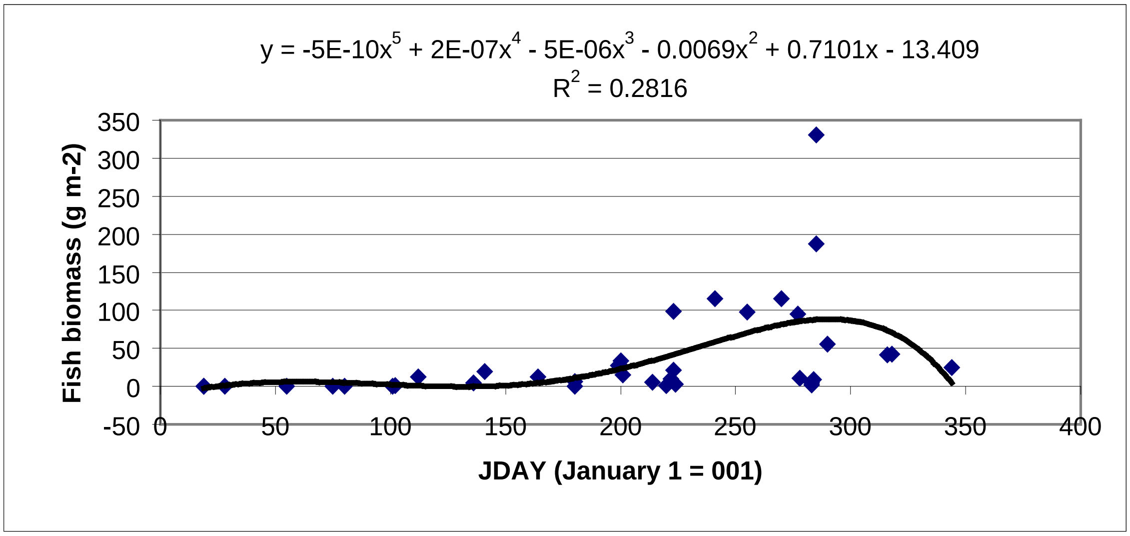
Figure 6: Polynomial regressions for fish biomass (g m^{-2}) in Flax Pond (data collected from 1971-1974)



a. Fish biomass at depths below 0.5 m



b. Fish biomass at depths of 0.5 m to 1.8 m



c. Fish biomass at depths above 1.8 m

Although winter flounder (*Pseudopleuronectes americanus*), mummichog (*Fundulus heteroclitus*), and Atlantic silverside (*Menidia menidia*) were caught most frequently and made the largest contributions to total biomass, we included 16 other species in our respiration calculations. These species are listed in Table 1.

Table 1: Size and names of fish captured in Flax Pond: 1970-1973

		Size (g)	
Common name	**Scientific name**	**Min.**	**Max.**
Atlantic alewife	*Alosa pseudoharengus*	1	78
American eel	*Anguilla rostrata*	1	1350
Atlantic menhaden	*Brevoortia tyrannus*	1	50
Atlantic Silverside	*Menidia menidia*	1	14
Atlantic tomcod	*Microgadus tomcod*	1	110
Winter flounder	*Pseudopleuronectes americanus*	1	812
Bluefish	*Pomatomus saltatrix*	1	74
Cunner	*Tautoglabrus adsperesus*	1	157
Sticklebacks	*Apeltes spp.*	1	4
Grubby	*Myoxocephalus aeneus*	1	37
Mummichog	*Fundulus heteroclitus*	1	40
N. pipefish	*Syngnathus fuscus*	1	7
O. toadfish	*Opsanus tau*	1	238
R. seabass	*Centropristes philadelphicus*	1	16
S. killifish	*Fundulus majalis*	1	44
S.searobin	*Prionotus evolans*	1	208
Windowpane	*Scophthalmus aquuosus*	34	325
Scup	*Stenotomus chrysops*	1	28
Tautog	*Tautoga onitis*	1	248
Anchovy	*Anchoa spp.*	1	5

Because we lacked quantitative information concerning the metabolism of the fish sampled in Flax Pond, we needed to use an equation from the literature to estimate total fish respiration. We chose an equation from Nixon and Oviatt (1973) that estimated fish respiration in g O_2 m^{-2} hr^{-1} in a Rhode Island bay. The equation predicts respiration based on wet weight of fish and temperature, which suited our needs nicely.

FishResp = FshBioM*(0.12*Temp+0.42)

Where FishResp = Fish respiration (g O_2 m^{-2} hr^{-1})
FishBioM = Depth-dependent fish biomass (kg m^{-2})

Each prediction of fish respiration was divided by four to give an estimate of respiration in g O_2 m^{-2} 15-min.$^{-1}$, which was our simulation time step.

Spatial Analysis:

As previously mentioned, a 6 x 6 m digital elevation model (DEM) was generated using hypsographic curves of the pond. The known depth values of the curves were then used to estimate unknown depth values in the marsh using a statistical interpolation known as kriging. Kriging estimates values based on their statistical relationship to known values. Although the statistical results of that exercise are not available to be included in this report, the small size of Flax Pond provides an opportunity to extrapolate accurate estimations of depth in the marsh. The landscape surrounding the pond with an elevation above 30 m was not accurately assessed, as hypsographic curves for those areas were limited. Considering that these elevations are not relevant to our analysis, we converted all the cells in the DEM that contained elevations of 25 m and above to null values. The resultant image was a 138 x 300 cell Idrisi raster file (Idrisi, Release 2) that included values for the high and low marsh of Flax Pond.

Our simulation model created a raster file for both water volume and oxygen concentration of each cell at each 15-minute interval of a given day. Thus, we were able to compare the spatial fluctuations of oxygen and water volume within the pond throughout each day of an entire year.

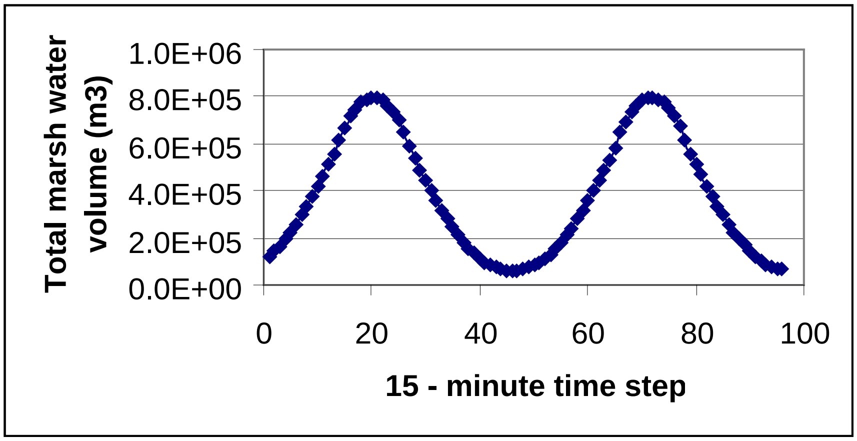
Results:

Our simulations of the distribution of dissolved oxygen in Flax Pond suggest that dissolved oxygen concentrations reach minimum values of 0 g O_2 m^{-3} during the night in July and August and peak at ~12 g O_2 m^{-3} near the mouth of the pond in January and February. Fucoid algae appear to be the biggest producers of oxygen in the marsh flats (8 g O_2 m^{-2} hr^{-1} in July), while *Spartina alterniflora* are the biggest consumers of oxygen at nighttime (1.2 g O_2 m^{-2} hr^{-1} in July). Dissolved oxygen concentration generally fluctuate more within the marsh and less at the marsh mouth, where the influence of Long Island Sound waters is more pronounced.

Tide Volume Simulation:

Our simulation of tidal volume predicted a total volume of water in the marsh to peak at nearly 800,000 m^3 (Figure 7) for a day in January.

Figure 7: Total volume of water in Flax Pond during January 1



This value varied above and below the 800,000 m^3 value, depending on whether the tide was spring or neap. The depth of high tide varied from 1.8 m to 2.1 m, as the magnitude depended on the timing of the 29-day spring-neap tide cycle.

Saturation value simulation:

Considering that our estimations of saturation value are important to dissolved oxygen predictions, we report the results of the saturation value calculation (Figure 8). Saturation value varies in response to temperature and is highest (10.62 g O_2 m^3) in January when temperatures are at a seasonal minimum.

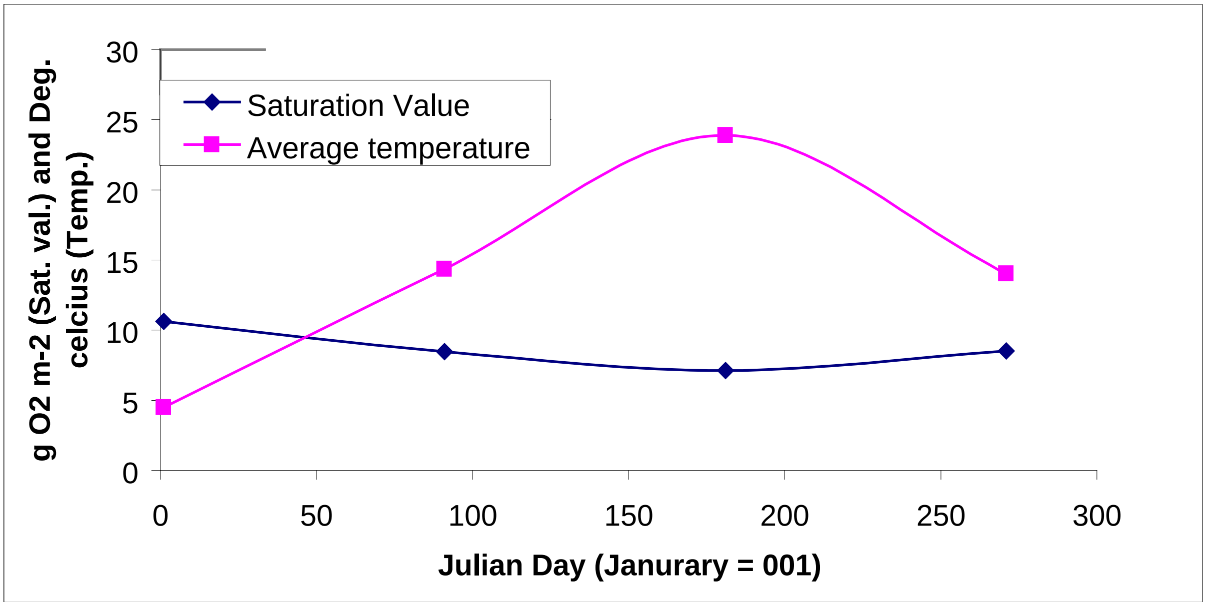


Figure 8: Saturation values and average temperature in Flax Pond throughout a year

Benthic photosynthesis and respiration:

Simulated benthic photosynthesis peaked at 0.44 g O_2 m-^{2} hr^{-1} at noon on July 1st, which is 4 times in magnitude greater than the January 1st noon peak of 0.137 g O_2 m-^{2} hr^{-1} (Figure 9). Respiration peaked on July 1st between 7 and 9 pm at 0.63 g O_2 m-^{2} hr^{-1}, when water temperatures in the marsh were highest. Respiration peaked between 0.05 and 0.1 at the same evening times on April and January 1st (Figure 9). Benthic communities were net producers of oxygen for 10 hours in January, 12 hours in April and October, and 16 hours in July. Although oxygen generation *via* photosynthesis was higher in July, respiration was also at a seasonal high during non-photosynthetic periods of the day at this time of the year. High respiration rates served as a draw down of oxygen during the night.

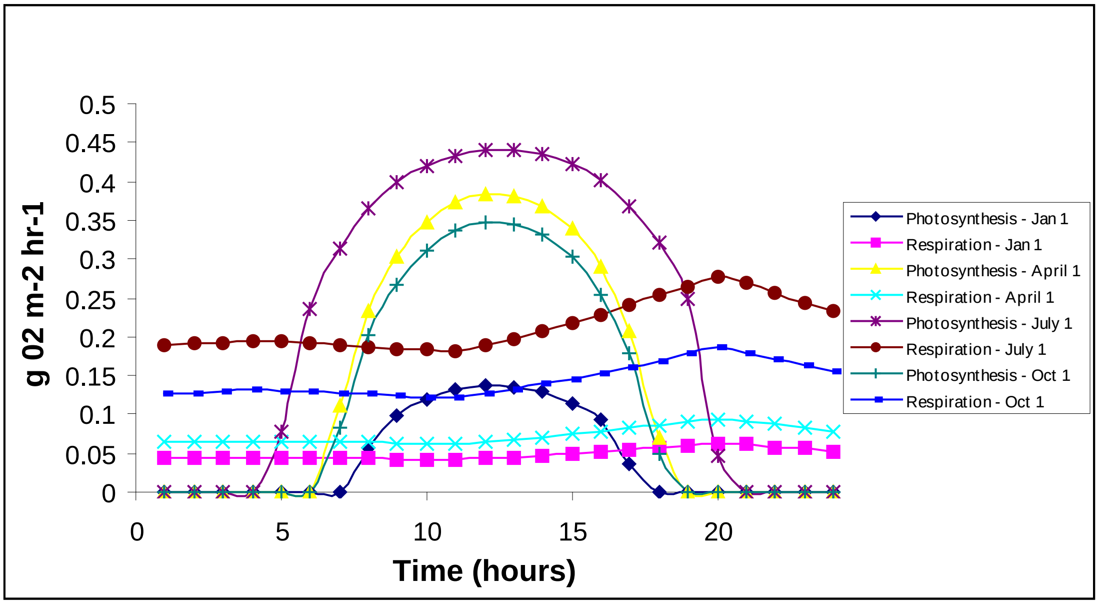


Figure 9: Seasonal and diel photosynthesis and respiration of Flax Pond benthic communities

Net oxygen production/consumption of S. alterniflora:

We report here the results of the total gas exchange of *S. alterniflora* with the atmosphere, not with the water column. Exchanges with the water column are not reported because they vary over short time and space intervals and are nearly impossible to generalize into a simple figure. Based on the water depths of the pond throughout a day, the exchange of *S. alterniflora* with the water column is 20-60% (on average) of the exchange with the atmosphere. The variation in net oxygen production/consumption of *S. alterniflora* stands with the atmosphere was highest in summer, with a noon peak of 2.296 g O_2 m-^{2} hr^{-1} produced and a night time minimum of 2.317 g O_2 m-^{2} hr^{-1} consumed (Figure 10). *Spartina* respiration was minimal in January, with 0.272 g O_2 m-^{2} hr^{-1} produced at noon and 0.275 g O_2 m-^{2} hr^{-1} consumed at near midnight.

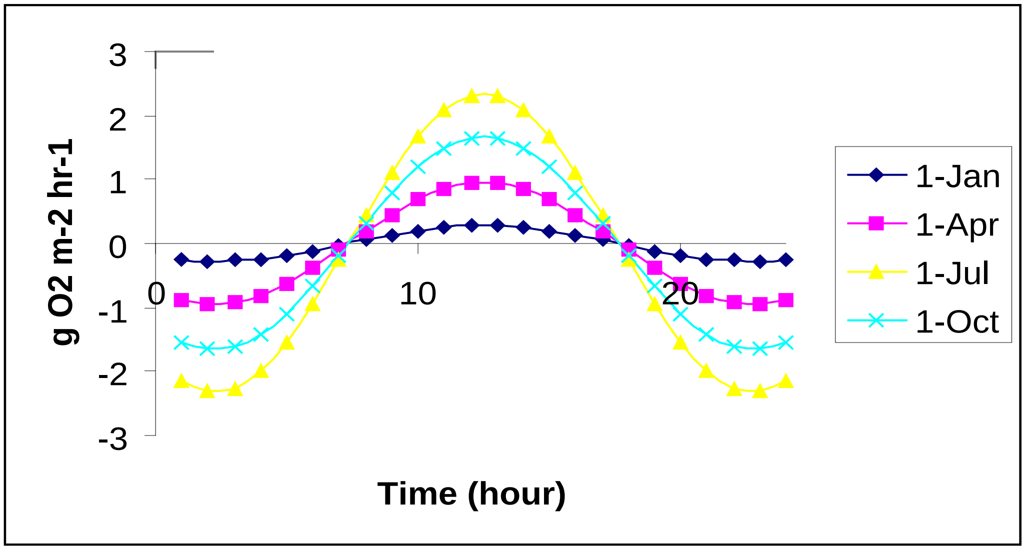
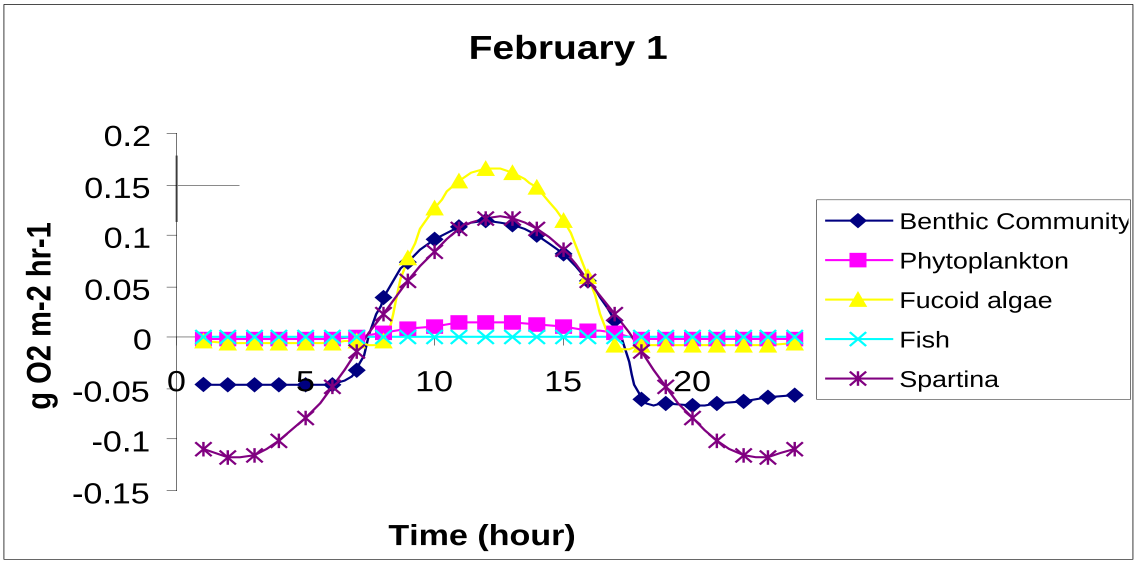


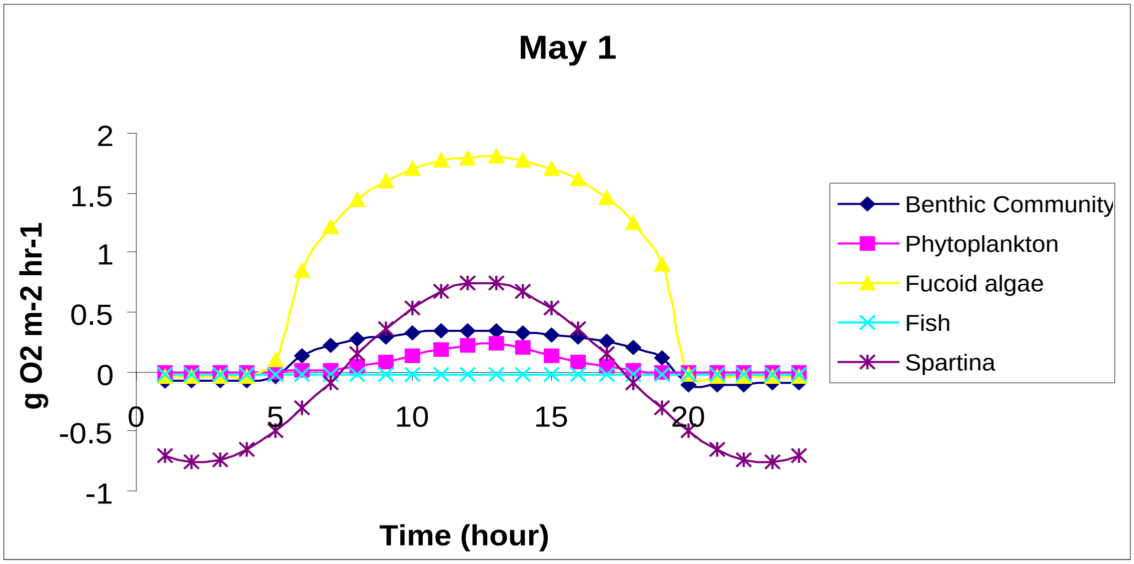
Figure 10: Seasonal and diel net oxygen flux associated with *S. alterniflora* photorespiration exchange with the atmosphere

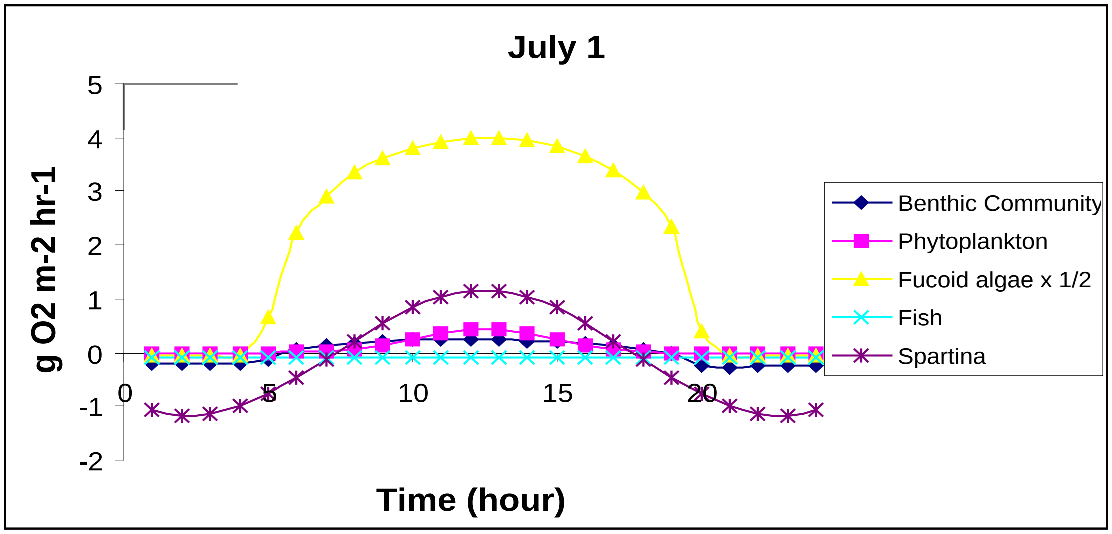
Seasonal metabolism of all biotic compartments:

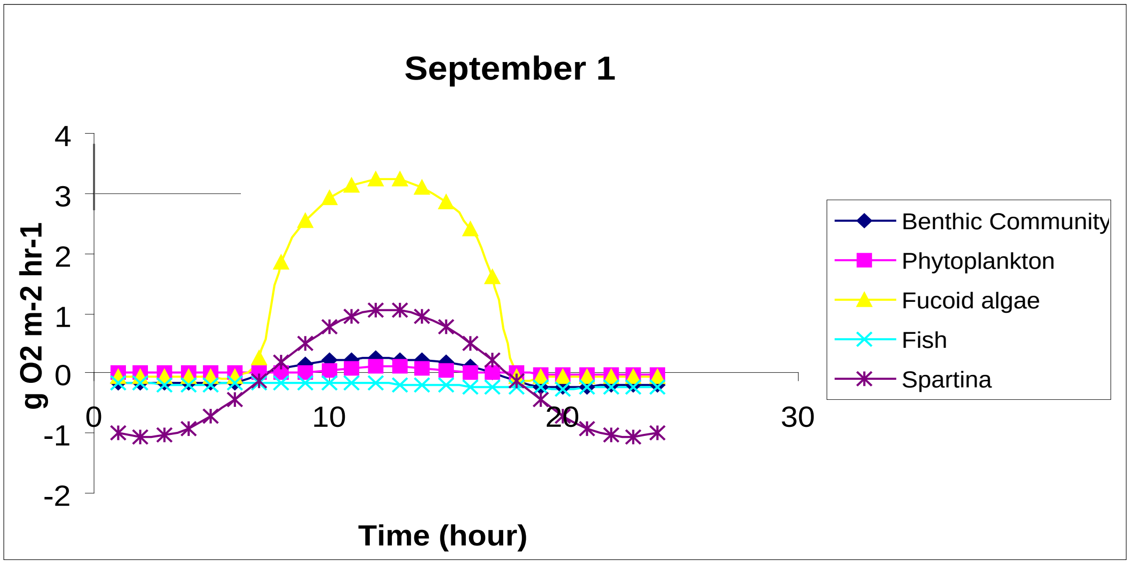
Our simulations of the metabolism of each biotic compartment varied in magnitude throughout the year, but hourly trends were often similar in different seasons. The seasonal and diel metabolism of *S. alterniflora* is not presented in this section, as *S. alterniflora* exchange varied throughout the pond. We report biotic metabolism for February 1, May 1, September 1, and December 1 (Figure 11).

Figure11: Simulated diel dissolved oxygen production/consumption by all biotic components of Flax Pond for four days of the year




May 1
g O2 m-2 hr-1
2
1.5
1
0.5
0
-0.5
-1
0
5
10
15
20
Time (hour)
Benthic Community
Phytoplankton
Fucoid algae
Fish
Spartina


July 1
g O2 m-2 hr-1
5
4
3
2
1
0
-1
-2
0
5
10
15
20
Time (hour)
Benthic Community
Phytoplankton
Fucoid algae x 1/2
Fish
Spartina


September 1
g O2 m-2 hr-1
4
3
2
1
0
-1
-2
0
10
20
30
Time (hour)
Benthic Community
Phytoplankton
Fucoid algae
Fish
Spartina

In spring and summer months, fucoid algal photosynthesis nearly 6 orders of magnitude higher than benthic and phytoplankton photosynthesis and contributed over 50% of gross production. Fucoid algal photosynthesis peaked in July when biomass was highest, with 8 g O_2 m^{-2} day^{-1} photosynthesis, while reaching a seasonal minimum of 0.675 g O_2 m^{-2} day^{-1} in January. Fucoid algae was therefore the greatest producer of oxygen in the regions of the pond where it existed.

Benthic photosynthesis was nearly equal to fucoid algal photosynthesis in late fall, winter and early spring months (October – March), at 0.13 g O_2 m^{-2} day^{-1}. In these colder months, combined benthic and fucoid algae contributed nearly 60% of photosynthesis. Benthic respiration exceeded fucoid algal respiration in all months of the year, as benthic respiration of fucoid algae peaked at 0.124 g O_2 m^{-2} day^{-1} in August, where benthic respiration was 0.6 g O_2 m^{-2} day^{-1} at the same time of the year. Seasonal respiration minimum for benthic communities was 1.175 g O_2 m^{-2} day^{-1}, and 0.118 g O_2 m^{-2} day^{-1} for fucoid algal in January. In tidal creeks, where fucoid algae and *S. alterniflora* were absent, benthic communities were clearly the greatest consumers/producers of oxygen.

Phytoplankton photosynthesis and respiration was 10-50% and 4-10% of benthic and fucoid algal photorespiration, respectively, throughout the year. The respiration of fish, though 0% of total metabolism from December to April, was non-trivial in late summer and fall. Fish respiration exceeded the combined respiration of phytoplankton and fucoid algae in September and October. Respiration rates of up to 0.25 g O_2 m^{-2} hr^{-1} were simulated in October, when combined fucoid algae and phytoplankton respiration was 0.215 g O_2 m^{-2} hr^{-1}.

Spartina alterniflora metabolism varied seasonally, with peak production of 1.3 g O_2 m^{-2} hr^{-1} in July and minimum production in January, at 0.12 g O_2 m^{-2} hr^{-1}. *S. alterniflora* contributed 40% of oxygen production in winter months (December to February), but only 20% in summer and late fall (June to September), when fucoid algal production was highest. These production estimates of *S. alterniflora*, when combined with the fucoid alga production suggest that production is much higher on the salt marsh flats than in tidal creeks.

Fish were only recorded in the pond in summer and late fall months (May – December), but their contribution to total ecosystem metabolism was small even when they were present. Fish respiration peaked at 0.24 g O_2 m^{-2} hr^{-1} in September and reached a minimum of zero many times during the year. During summer days, fish respiration composed less than 1% of net ecosystem metabolism during sunlit hours, but was much more important in the oxygen dynamics of the pond after sundown. The peak respiration rates of fish in summer and early fall were comparable to benthic communities, phytoplankton, and fucoid algae, assuming fish are present in the pond. At a period late in the day of September 1, fish respiration was 0.25 g O_2 m^{-2} hr^{-1}, while the sum of benthic, phytoplankton and fucoid algae respiration was 0.27 g O_2 m^{-2} hr^{-1}.

Seasonal and yearly P:R ratios:

The ratio of production to respiration (g O_2 m^{-2}) provides for an indicator of whether the Flax Pond ecosystem is a net producer or consumer of oxygen. Seasonal P:R ratios of Flax Pond indicate that some of the biotic components of the pond are net consumers of oxygen in some parts of the year, while others are consistently net producers of oxygen. P: R ratios are presented for single days of the year.

Disregarding fish, which do not engage in photosynthesis, benthic communities were the only biotic component of the pond that were a daily net consumer of oxygen for single days. Each biotic compartment that included plants was a net consumer of oxygen in periods of the day when no sunlight was present. The benthic compartment was a net consumer of oxygen in January, December, and late fall months, while fucoid algae and phytoplankton were net producers of oxygen at all times of the year (Table 2).

Table 2: Daily P: R ratios for three biotic compartments of Flax Pond (g O_2 m^{-2} day^{-1})

JDAY	Benthic Community	Phytoplankton	Fucoid algae
1	0.89	6.73	5.72
31	1.04	4.74	7.95
61	1.16	6.06	10.19
91	1.94	7.72	18.01
121	2.34	12.18	26.65
151	2.17	12.71	34.82
181	1.04	11.49	35.80
211	0.79	6.95	24.56
241	0.84	5.43	182.38
271	0.87	4.52	9.77
301	1.63	3.68	7.43
331	0.88	3.85	5.70

Fucoid algal P: R was extremely high in July – September, and was also high relative to P: R ratios for benthic communities and phytoplankton. Benthic community and phytoplankton P: R ratios were highest between May and July. In the case of tidal creeks, where *S. alterniflora* and fucoid algae were absent.

Yearly P:R ratios illustrate some of the same trends we observed with the daily values. The P: R ratios for the accumulated yearly metabolic activity of benthic communities, phytoplankton, and fucoid algae (calculated from monthly averages) are 1.21, 8.99, and 26.71 g O_2 m^{-2} yr^{-1}, respectively. The low P: R ratio of benthic communities exhibits the intense respiratory activities reported by Hall *et al*. (1979).

The estimates we have made for all components of Flax Pond allow us to calculate net primary production (NPP), which offers a measure of the total metabolism of the ecosystem. Calculations of NPP (in g O_2 m^{-2} yr^{-1}) can therefore indicate whether the pond as a whole in a net consumer or producer of oxygen. We present NPP estimates without the contributions of *S. alterniflora*.

$$\begin{array}{ccc} NPP\ (\mathrm{g\ O_2\ m^{-2}\ yr^{-1}}) & = & GPP\ -\ RP \\ \mathbf{3358} & & \mathbf{4116\ -\ 758} \end{array}$$

Yearly estimates of production and respiration were made estimating an average of monthly P and R. Clearly the pond is a net producer of oxygen, but this net production is likely not characteristic of all regions of the pond.

We made similar NPP calculations in terms of carbon for Flax Pond.

$$\begin{array}{ccc} NPP\ (\mathrm{g\ C\ m^{-2}\ yr^{-1}}) & = & GPP\ -\ RP \\ \mathbf{1260} & & \mathbf{1544\ -\ 284} \end{array}$$

The calculations are based on the simplified stoichiometric equation for photosynthesis:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

Spatial analysis:

We present the spatial distribution of dissolved oxygen in Flax Pond at high and low tide for the first day of each month for an entire year (Figure 12 a-l). We found little spatial variation during winter months (December – February), which are times when the metabolic activity of Flax Pond is low. Dissolved oxygen concentrations varied from 0 g O_2 m^{-3} to just above 12 g O_2 m^{-3} at given times of day from March – November.

In most months, dissolved oxygen concentrations were lower on average at low tide than at high tide (Figure 12). The low tides displayed in figure 12 occurred during the morning (midnight to 6 AM), non-sunlight hours, while high tides occurred during late morning to early afternoon hours (8 AM to 2 PM). The low oxygen values for a given portion of the pond were found frequently in areas of the pond where the substrate is mud and gravel and little or no *S. alterniflora* were present. Oxygen concentrations were also ~1.5 times higher in waters near the inlet to Long Island Sound, where the influence of oxygenated ocean waters was more intense (Figure 12).

Discussion:

Seasonal metabolism of all biotic compartments:

Our appraisal of the photosynthesis and respiration of several biological compartments in Flax Pond permits us an opportunity to explore how biological variables affect prevailing dissolved oxygen concentrations in the pond. A discussion of the spatial distribution of the various biological compartments will allow us to synthesize the affects of these compartments on the oxygen dynamics of Flax Pond.

Fucoid algal Photorespiration:

We are confident in our estimations of fucoid algal metabolism, as we had access to a large seasonal dataset of biomass and photosynthesis/respiration, much like the fish and benthic data. We did make a simple assumption that only *Ascophyllum nodo*sum ecad *scorpiodes* was found alone in the salt marsh flats, not accompanied by the similar alga *Ascophyllum nodo*sum ecad *mackaii.* We did not include *A. nodosum* ecad *mackaii* because its distribution is constant seasonally and because it inhabits the tidal creeks of Flax Pond, were benthic metabolism studies were carried out (Brinkhuis 1976). These benthic metabolism studies accounted for any fucoid algae in the tidal creeks.

We have simulated fucoid algae to contribute significant amounts of dissolved oxygen to Flax Pond waters during summer months. One's first impression of that feature might be that fucoid algae play a significant role in the oxygen dynamics of the pond. Although their role is certainly not trivial, they are only found on the marsh flats and not within the tidal creeks. This fact is illustrated in the spatial images of figure 12, as oxygen concentration often remains higher on the marsh flats than within the tidal creeks (figure 12). Along with the photosynthetic contributions of *S. alterniflora*, waters in the marsh flat remain oxygenated during sunlit periods of the day. Conversely, the respiration of algae is proportionally lower than that of photosynthesis (Figure 11). It appears that this aspect of the simulation is what prevents the marsh flats from going anoxic during non-sunlight hours.

Phytoplankton:

Phytoplankton are considered to make small contributions to the oxygen dynamics of Flax Pond, as production composed less than 3% of total marsh production for a year. Our simulation did fall short of the measured values by Moll (1977). Phytoplankton was found to produce 11.7 g C m^{-2} yr^{-1} by Moll (1977), while we simulated 3.67 g C m^{-2} yr^{-1}. We can accept this underestimation, considering that phytoplankton will still contribute less than 10% of total marsh production if simulated at the measured values.

Benthic Metabolism:

Hall *et al.* (1979), who studied the benthic metabolism of the Flax Pond ecosystem, noted that 1/3 of aquatic photosynthesis was the product of benthic organisms. Our simulations generally provide the same result, as benthic production composed 30% of total production from December to February and nearly 20% in the spring. Hall *et al.* (1979) also noted that benthic photosynthesis was closely correlated to solar radiation. Our simulations account for this observation, as sunlight is the only forcing function on benthic photosynthesis. During summer month, fucoid algal production was high enough that benthic photosynthesis composed less than 20% of aquatic photosynthesis. Our simulations only consider benthic and phytoplankton photosynthesis to be occurring in the tidal creeks, thus benthic photosynthesis is actually contributing nearly 80% of total aquatic photosynthesis in these regions of the pond. We conclude that oxygen dynamics in Flax Pond are slightly more complex than some preliminary assessments. Variation in the distribution of plant types plays a large role in the partitioning of photosynthetically derived oxygen between *S. alterniflora*, fucoid algae, benthic communities, and phytoplankton.

We have observed drastic peaks and troughs in the benthic oxygen data from Flax Pond that have occurred for short periods of the day. For example, 1-hour peaks in dissolved oxygen were observed in benthic communities at night, which we attribute to the inundation of Flax Pond with tide water from Long Island Sound. Our simulations of benthic oxygen changes do not account for this, but our predictions of free water oxygen variations do account for tidal effects. Our simulations of benthic metabolism only include the activities of the biota, while the measured data compared the oxygen concentration in the free water with water enclosed in a benthic chamber.

Spartina alterniflora metabolism:

The metabolism of *S. alterniflora* has been outlined in various sections of this report and we will only outline a few key point of its contributions to the oxygen dynamics of Flax Pond. Net primary production of *S. alterniflora* was measured to be roughly 400 g C m^{-2} yr^{-1} in Flax Pond (Woodwell et al. 1973), which exceeds that of fucoid algae, which is on average, 75 g C m^{-2} yr^{-1} (Brinkhuis 1976). These data suggest that *S. alterniflora* would contribute more to the free water oxygen dynamics of Flax Pond, but in fact we find this not to be the case. Fucoid algae and *S. alterniflora* contributed equally to a combined 80% of total production in the salt marsh flats in fall and winter. In the summer (June-August), however, fucoid algae contributed more oxygen to the waters of Flax Pond than *S. alterniflora*. We can resolve this unexpected result because we know that only the non-emergent portions of stalks of S. *alterniflora* exchange with the waters of Flax Pond, while the entire biomass of fucoid algae exchanges with the water column.

Fish Respiration:

We consider our estimations of fish respiration to be reasonable because we have a large seasonal dataset of fish biomass. Our regression equations are also accurate, even though in using them we dismiss the possibility that an unusually large number of fish are in Flax Pond at a given time. Instances of extremely high fish biomass were restricted to summer months and perhaps were a sampling anomaly resulting from the existence of one or a few large, spawning fish. Salt marshes and to some extent, all coastal brackish wetlands, are noteworthy locations of saltwater fish spawning grounds (Teal and Teal 1969, Douglass and Stroud 1971, Woodwell *et al*. 1973, Day *et al*. 1973). The characteristics of the fish found in Flax Pond seem to parallel this perception, as many of the fish captured were less than 5 g in weight.

Although fish respiration composed a small fraction of total ecosystem metabolism for much of the year, we included it in our analysis because the biomass of fish in the pond was quite high for a period of 3-5 months in late summer and early autumn. In comparison, the fish biomass recorded in Flax Pond is higher than many other systems in the United States (Table 3).

Table 3: Fish biomass in various aquatic ecosystems (based on Nixon and Oviatt (1973))

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	4.0 - 15	Hyle (1971)
Winter	3.0 - 6	
Summer	3.0 - 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	Nixon and Oviatt (1973)
Late summer with menhaden	28	
Fall	7.0 -14	
Winter	5	
Flax Pond Marsh, Long Island, N.Y.		
Winter	0 - 0.5	This study
Late summer	60 - 100	
Fall	10.0 - 50	

Production/Respiration ratios:

Our analysis of the biota of Flax Pond, using P: R ratios provide us with an opportunity to gain additional insight into the dynamics of Flax Pond. Hall *et al*. (1979) found that P: R ratios in benthic communities were generally below 1.0 (mean = 0.7), indicating that respiration exceeds production. This preliminary analysis agrees with our simulations, as we observed similar P: R ratios in winter and fall months of 0.89 (January), 0.79 (August), and 0.87 (October). We did simulate positive P: R ratios in June and July, which suggests that we have either underestimated respiration or over estimated photosynthesis during these months. We consider an underestimation of respiration to be the case, as our spatial images often display that dissolved oxygen concentrations rarely fall below 2 g O_2 m^{-3} during the summer. Hall *et al*. (1979) suggested that summer values of dissolved oxygen in many regions of the pond fell below 2 g O_2 m^{-3} at low tide.

This underestimation of respiration may also be playing a role in inconsistencies between of our estimations of NPP and those reported by Woodwell *et al.* (1973). Our simulations yield a NPP values of 1260 g C m^{-2} yr^{-1}, while Woodwell *et al*. (1973) measured 535 g C m^{-2} yr^{-1}. This rather large discrepancy is possibly the result of an underestimation of respiration, but also may be due to an overestimation of production. The simulated net production of fucoid algae was extremely high and may have artificially increased our estimates of gross primary production (GPP).

Spatial analysis:

The general trend we find in our spatial simulations of dissolved oxygen in Flax Pond is a reduction of oxygen in the tidal channels of the pond (Figure 12). We are familiar with our simulations and we know that benthic and phytoplankton photosynthesis were the only biotic contributors of dissolved oxygen to the regions they are found in. It therefore appears that dissolved oxygen concentrations are lower in the tidal creeks because photosynthetic additions are lower. Another common trend is that dissolved oxygen concentrations tends to be higher at the marsh inlet and lower in regions further from the influence of Long Island Sound (figure 12). As mentioned previously, the regions of the pond nearest to Long Island Sound are relatively more subsidized in respect to oxygen than other reaches on the pond. The biological activities within the regions Flax Pond that are far from Long Island Sound do not receive this subsidy, and therefore have lower oxygen concentrations from those at the inlet.

Tidal effect on dissolved oxygen:

In a situation like we find in Flax Pond, the effects of the tide can play a large role in the prevailing oxygen concentrations at a given part of the pond. The coupling of metabolic activities to the height of the tide can result in unexpected dissolved oxygen concentrations at a given point in time. As illustrated in figure 12, we see that dissolved oxygen concentrations are lower at high tide than at low tide on July 1. We would expect that oxygen concentrations would be lowest at low tide, when the influence of waters saturated with oxygen is lowest. We in fact find that oxygen concentrations are higher at low tide. We may resolve this problem because low tide occurs when photosynthesis is high, and it appears that photosynthesis generated oxygen is compensating for the lack of ocean-derived oxygen. The situation is further complicated by the fact that the saturation concentration of oxygen is lower in July. Thus, any ocean-derived waters will contain less concentrated oxygen in July than they would in December.

We also observe unexpected peaks in measured diel oxygen at times of the day when sunlight is not present (see figure 12). We can only explain these fluctuations as resulting from the movement of tide waters through Flax Pond and increasing the oxygen concentration.

General limitations of the model:

We understand that all models are simplifications, but models often provide critical information to research, as they allow one to formulate what they do know about a system. One of the primary limitations, or rather simplistic features, of the model is the fact that the forcing functions on Flax Pond are only temperature, sunlight, and time. The model would become more versatile if the biological components of the system could be simulated as a function of the nutritional conditions in the pond (i.e. nutrient and food availability). Yet, we are able to make quality estimations of the biological components in Flax Pond because we have such a comprehensive, time-series dataset.

The model also limits us in that the raster file we use in our analysis was created in an older version of IDRISI years ago, using a geospatial statistical technique known as kriging. A bathymetric map of Flax Pond was available and was used as the source of data to produce the raster image. Kriging was used to estimate unknown depth values in the marsh where no data was available. An output of the error involved in this routine is generated following the analysis, but we do not have access to that output. We are therefore not certain as to how rigorously generated and/or accurate the image we used is. Our predictions of total water volume in the marsh do agree quite well, however, with calculations made by Woodwell and Pecan (1973) using stereoscopic aerial images.

Lastly, out water flow simulation is somewhat crude, as we avoided applying complex mathematical formulations of mixing and flow rates to the tide water in our model. We do argue that our simplification is valid, as our technique serves our purpose in moving oxygen concentrations through the pond. The absence of a freshwater inflow to the marsh further allows for such a simplification.

Validation:

Diel benthic oxygen fluctuations:

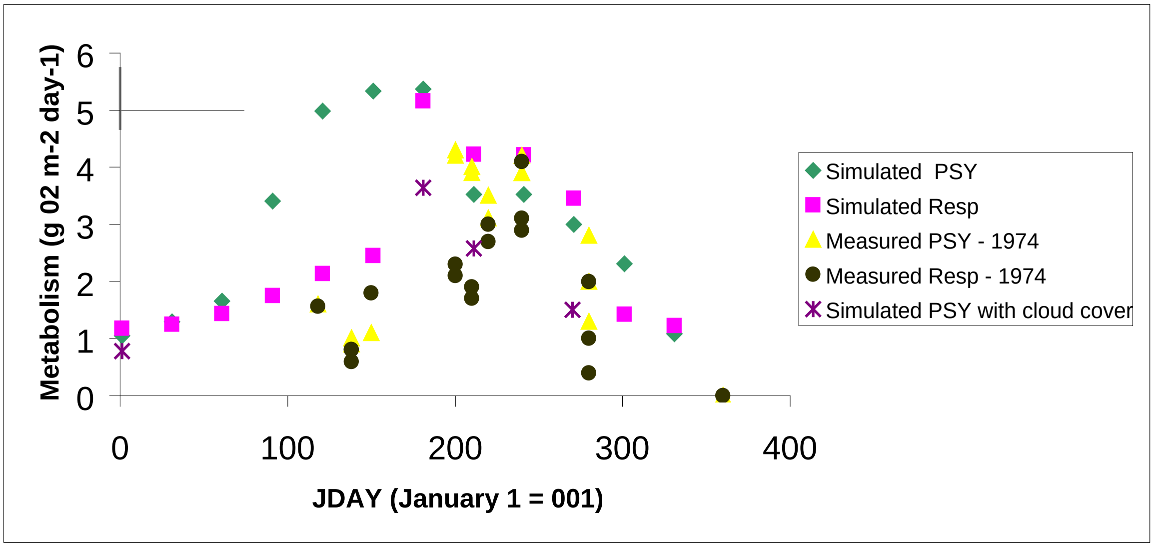
We were able to compare our simulations of benthic oxygen fluctuations with measurements of hourly oxygen fluxes from 1971-1974 (see Hall *et al*. (1979) for representative datasets). Although we found general agreement of our simulation with measured values, there were some significant discrepancies between measured and predicted oxygen values (Figure 13 a-f).

Some of the error in the simulations is the result of variables that we do not have control over, such as unpredictable changes in cloud cover and water turbidity. Examples of turbidity include suspended organic matter and colored dissolved organic matter (CDOM), which we do not have measurements of. Although we generated a stochastic cloud cover variable, we considered any days to have cloud cover to have consistent cover throughout the day. We realize, of course, that most cloudy days include some periods of sunshine, but we have no basis to estimate the number of hours in a day that clouds cover the sky.

The inflow of water from Long Island Sound in non-sunlight hours can also cause oxygen values to rise when there is no production of oxygen in Flax Pond itself. The simulations we present in figure 13 do no incorporate the oxygen added to benthic communities by Long Island Sound waters. Thus, our validation is limited in that we only predict the biologically derived oxygen, whereas the measured benthic chamber oxygen values include Long Island Sound-derived oxygen.

We also compared our simulation of cumulative total daily photosynthesis with measurements taken in 1974 (illustrated in Hall *et al.* 1979). Our results agree quite well with the measured data in winter and summer months, but we overestimate photosynthesis in spring (Figure 14). Simulated photosynthesis more closely agreed with measured values when we simulated the amount of incoming solar radiation blocked by clouds (Figure14). We are not surprised by this result, as clouds cover some portion of the sky for much of the year in New York State.

Figure 14: Daily photosynthesis and respiration in Flax Pond throughout a year

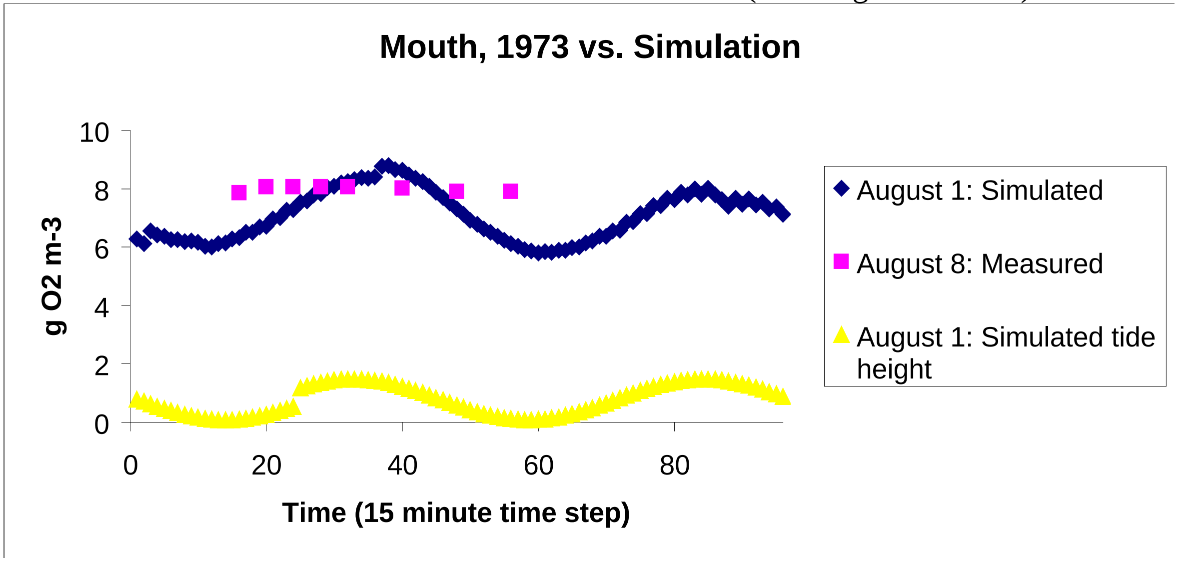


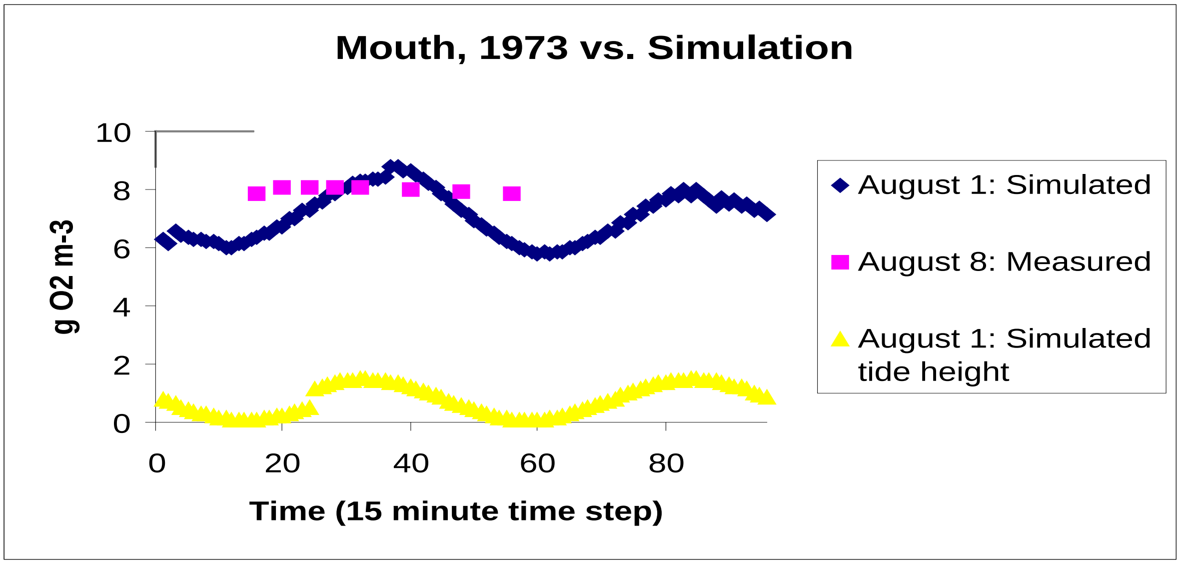
Spring conditions in New York State are especially cloudy relative to other times of year, which is likely the reason why we overestimate photosynthesis at this time of year. The addition of cloud cover to solar insolation estimates produces photosynthesis values that agree well with the measured data from Flax Pond (Figure 14).

Validation of open water simulations:

A series of measurements of open water dissolved oxygen concentrations are available for the inlet washing into Flax Pond and at a point below a bridge located within the pond. We have taken advantage of this data and compared our simulations of open water dissolved oxygen concentrations (Figure 15). The validations are for four separate days, with two validations at the bridge and two at the mouth.

Figure 15: Validation of simulated free water dissolved oxygen concentrations with measured values from the mouth of Flax Pond (tide height in meters)



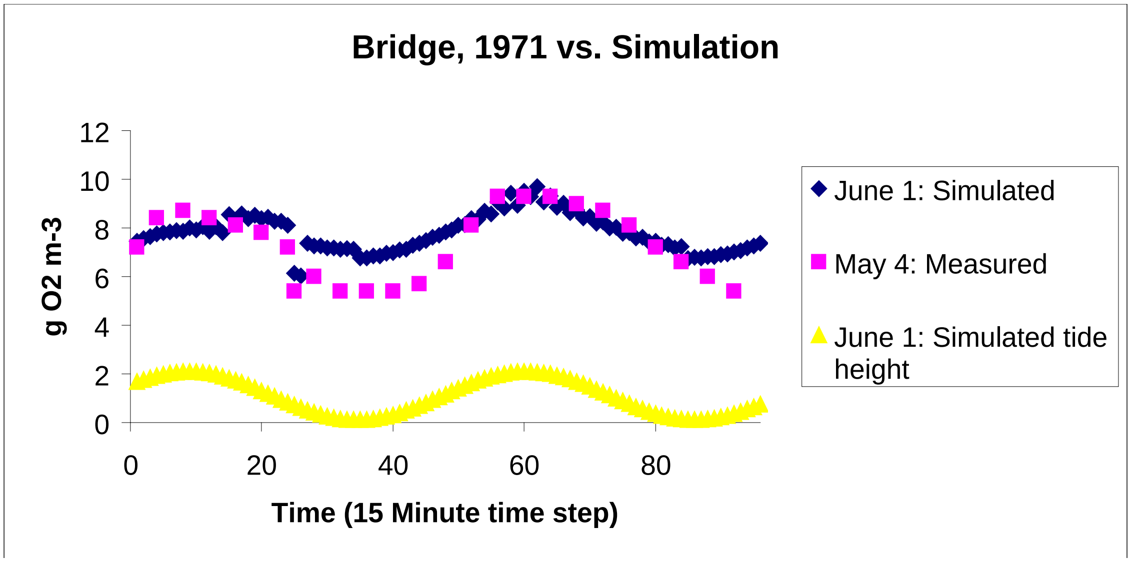


Although our simulations at the mouth on October 1 are quite similar to those measured in on October 3, 1973, it appears that we predict a much larger diel variation in dissolved oxygen concentration at the mouth on August 1. Our error here is obvious (Figure 15), but we learn that oxygen concentrations in this reach of the pond are heavily influenced by the adjacent ocean waters. Our simulations consider the concentration of oxygen at the mouth to be sensitive to biological activity, yet it appears that this is not the case. We could attempt to explain this problem, and perhaps the biological activity in this part of the pond is low. The tidal current is probably most exaggerated in this section of the pond, and this stress could possibly make the standing crop of benthic organisms much less. Distinct zonation patterns are common in salt marshes, and zonation is generally though to result in response to a gradient in stress (Whittaker 1967, Barbour *et al*. 1980). The one or few stress tolerant species that inhabit similar sections of the marsh may be in low abundance, and there may be no species that can survive the conditions and replace them. The abundance of fish, which we assumed to be the same in all reaches of the pond at a given point in time, may also be lower here than inside the pond.

Our overestimation of the contribution of biological activity to free water dissolved oxygen concentrations at the mouth of Flax Pond is curious, as we sometimes underestimated these variations further within the pond.

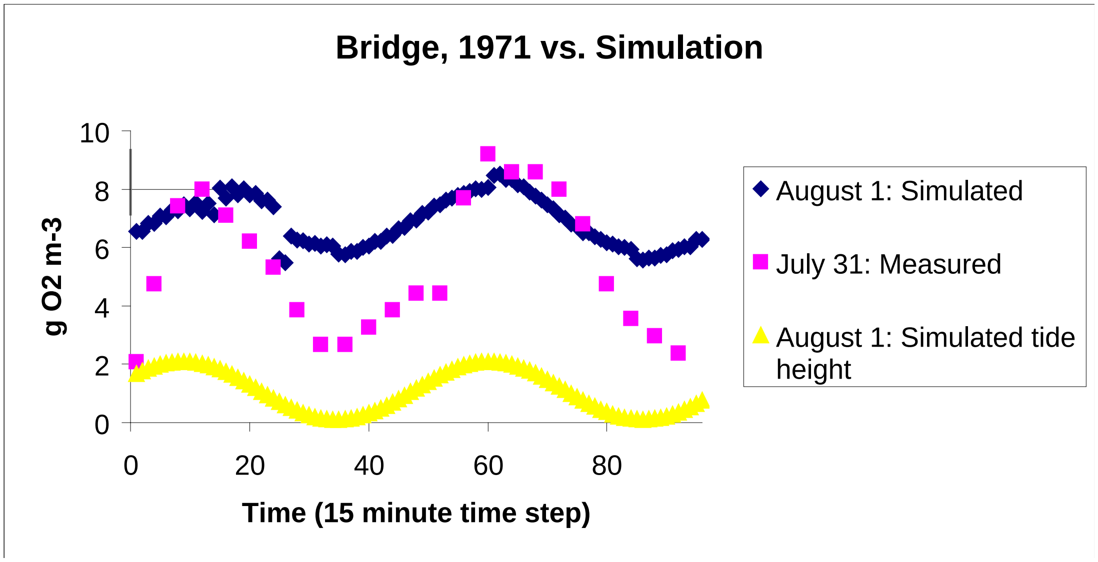
Our simulations of dissolved oxygen in the free water at the bridge agree quite well with measured values from May-June of 1971, but there are some small (1 g O_2 m^{-3}) inconsistencies (Figure 16). We could surely explore the reasons for the small differences between simulated and measured data from May-June, but the difference is likely the result of some stochastic variables, including cloud cover and turbidity.

Figure 16: Validation of simulated free water dissolved oxygen concentrations with measured values from a bridge within Flax Pond (tide height in meters)



Our simulations are less accurate on August 1st compared with measured data. One discrepancy between our simulations and the measured data is that measured oxygen concentrations fall 1.5 g m^{-3} below those which we simulated on August 1. Apparently the summertime respiration is actually more intense than we have simulated.

Figure 17: Validation of simulated free water dissolved oxygen concentrations with measured values from a bridge within Flax Pond (tide height in meters)



Another interesting aspect of both our simulations and the measured values is the matching of the peaks and troughs of dissolved oxygen with those of the tide water. Clearly the tide is playing a critical role in the oxygen dynamics of the pond, as oxygen values increase when high tide comes in (i.e. oxygen saturated waters are entering the pond).

Sensitivity Analysis:

The only forcing functions in our Flax Pond model are temperature, sunlight, and day of the year. Considering that sunlight and day of year are somewhat rigid parameters, we will only consider the effect of changes in temperature on the oxygen dynamics of Flax Pond. We therefore present the results of simulated temperature increases on the seasonal and diel dissolved oxygen dynamics of the pond. We will present the results of that sensitivity analysis on three days of the year: April 1st, July 1st, and October 1st.

There are expectations that global temperatures will rise 1.5-4.5°C when the atmospheric CO_2 concentration doubles in the next 100 years (Mahlman 1997). Assuming that these estimates are high, we will simulate an increase in monthly average water temperature of 2°C. A simulation of this sort not only provides an interesting glimpse into the effects of future climatic change on coastal ecosystems, but also provides an opportunity for us to test the sensitivity of our model to an important forcing function.

The simulated increases in temperature had little or no effect on photosynthesis, with a maximum 0.1% increase (g O_2 m^{-2} hr^{-1}) in benthic photosynthesis and less for other biotic compartments. Conversely, respiration increased an average of 10% in benthic communities, 7% for fish, 3% for phytoplankton, and 25% for fucoid algal communities. The increases in respiration were slightly more exaggerated in summer, as they were nearly double the winter increases (Figure 18).

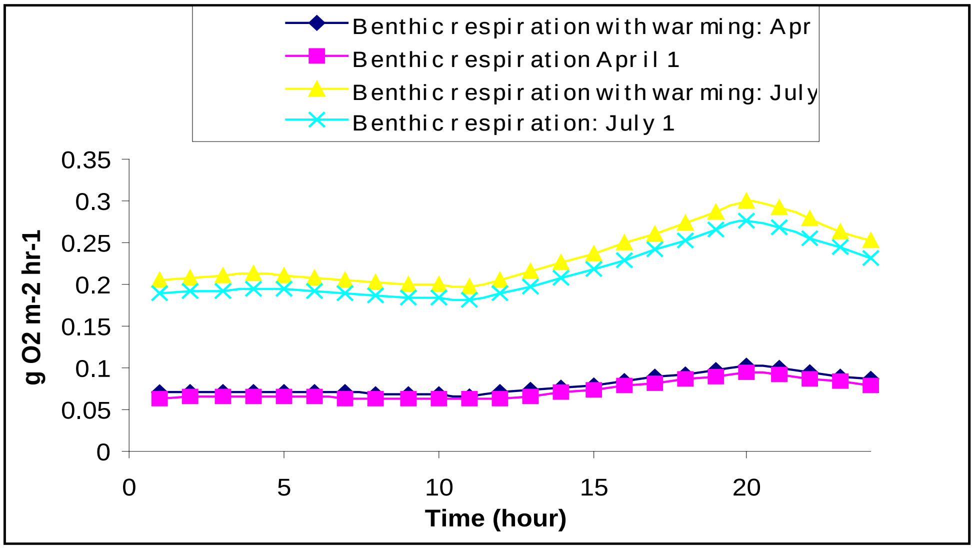
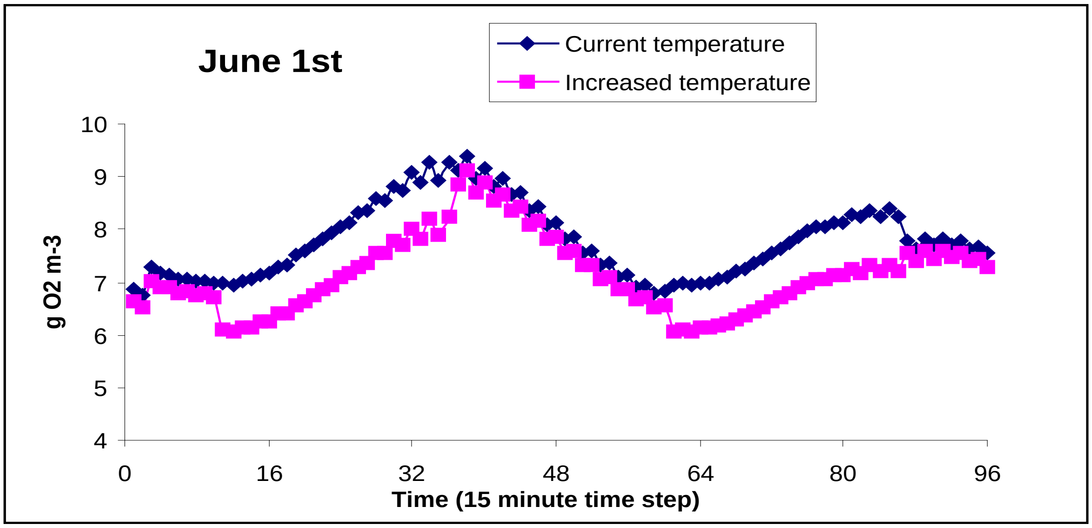
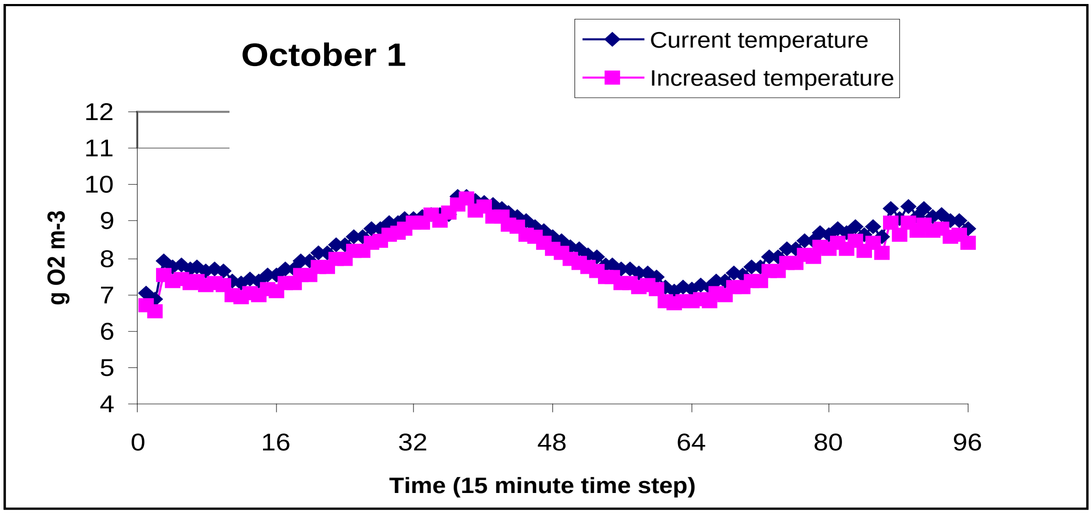


Figure 18: Respiration of Flax Pond benthic communities at current temperatures and simulated 2°C increases in average temperature

Free water simulations of dissolved oxygen are also lower than those simulated under the present temperatures (Figure 19). Again, we see how these fluctuations are more pronounced in summer months (June) relative to other seasons (October 1). We see how temperature-induced increases in photosynthetic activity are much lower than oxygen - consuming increases in respiration.

Figure 19: Effects of simulated temperature increases on diel oxygen dynamics in the free water of Flax Pond





Such increases in respiration could significantly alter the net metabolism of Flax Pond. Net production of the system would decrease and the demand for oxygen on the biota would be greater. The possibility that oxygen concentrations could drop below that needed to support aerobic life is possible, as there would not be a concomitant oxygen increase from photosynthesis. We do have to consider the oxygen subsidy of Long Island Sound, which will probably remain constant with a temperature increase. The only decreases in the oxygen concentration of Long Island Sound would be a reduction of the saturated oxygen concentration.

Although it would be equally interesting to model the effects of increasing sea level rise, it appears that any rises associated with increasing surface temperatures would not be a problem for Flax Pond. Sedimentation rates in Flax Pond, which were measured using ^{210}Pb dating, indicate that accretion rates in Flax Pond are 0.47-0.63 cm yr^{-1} (Armentano and Woodwell 1975). The highest estimates of sea level rise reported by Douglas (1991) and Mahlman (1997) are 75 cm total by the year 2100.

Future Work and Model Improvement:

The simulation model presented in this report has led us to a substantial number of conclusions about the Flax Pond ecosystem and has allowed us to visually illustrate what we know about the pond. This investigation does leave some questions left unanswered and our model requires some enhancements.

As mentioned in the methods section, our approach to simulating the inflow of the tide was to fill up cells in the raster file whose elevation was lower than the simulated tide height. We have successfully moved an accurate volume of water in and out of the pond this way, but have failed to account for some topographical features of the marsh. Some areas of the marsh may be lower than the tide height at a given point in time, but a raised area is preventing water from moving into the depression. The result is that a small pocket of water fills up in our spatial files that wouldn’t be filled if we went to Flax Pond tomorrow (Figure 20).

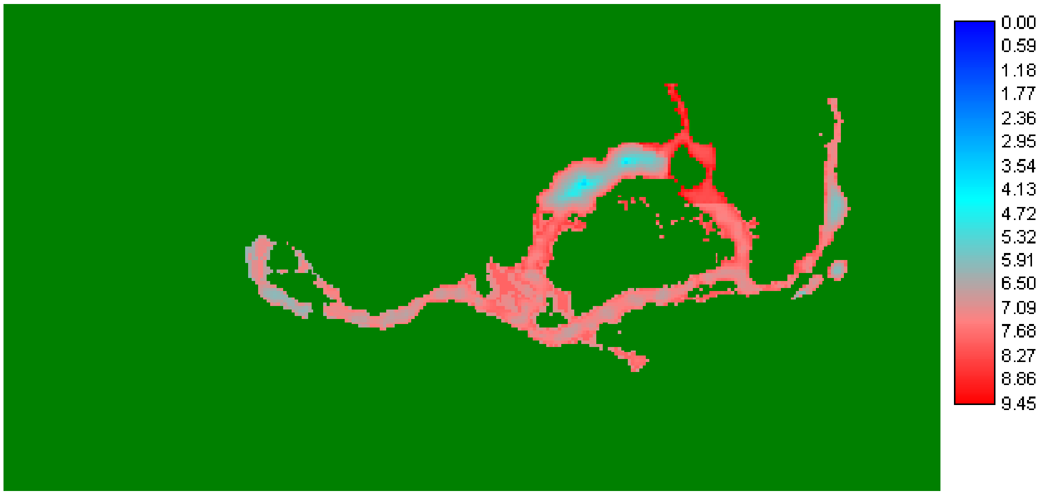


Figure 20: Spatial distribution of dissolved oxygen in waters of Flax Pond (note areas isolated from main water body)

A similar problem results when the tide exits the pond. During normal tide cycles in Flax Pond, small depressions are left filled with water when the tide recedes at low tide. These depressions are included in our model and can be seen in our spatial images (Figure 12 a-l), but we do not properly simulate the oxygen dynamics within them. Isolated depressions are temporarily cut of from the stress/subsidy of Long Island waters, which includes additions of dissolved oxygen. In the case that a depression is left in the evening, dissolved oxygen concentration will decrease rapidly as respiration consumes any oxygen left in waters of the depression. Our model considers these cells open to the waters of Long Island Sound and therefore provides them with oxygen subsidies.

We are missing these features of Flax Pond oxygen dynamics because we do not yet have the means to locate these small depressions in our raster file. I will propose a method to do this that can be incorporated into later versions of the model. The proposed procedure would include the following features:

1. Scan the neighboring cells of each cell in the file and read the elevation of those cells
2. Scan three layers of cell outside each cell
3. If all cells in a complete layer (out of the first three) around the cell have a higher elevation, we assume this cell to be isolated

4. Disconnect this cell from Long Island Sound waters when it fills with water

Validation is the one true way a model can be scrutinized in a way that allows for one to decide if it is good representation of the system, or if it requires improvement. Although we have presented our validation procedure in a previous section of this report, the tests were not as rigorous as we would have hoped. We have shown that we are satisfied with our simulations of the various biotic processes in the pond, but the tide model has really not been validated. We must travel to Flax Pond and take diel oxygen measurements at various points in the pond. A comparison of these points with our spatial and temporal predictions will provide us with the information we need to asses the quality of the model.

Conclusions:

We can gather from the validation of our simulations that our model requires some enhancement. Improvements in the accuracy of the respiration rates of benthic communities and fucoid algae may provide for larger reductions in dissolved oxygen concentration in several reaches in the pond in summer. We do observe some interesting spatial trends, as oxygen concentrations in the marsh flats appear to remain higher than those concentrations in the marsh flats. We observe this as a result of higher photosynthetic rates of the *S. alterniflora* and fucoid algae found on those flats. This has implications for fish production in the pond if fish preferentially utilize the tidal creek habitats. Interestingly, fish abundance is lowest in winter when dissolved oxygen concentrations are highest and most consistent. This may lend evidence to the claim that only young, newly born fish are found in the pond after they hatch from summer spawning runs.

The tidal creeks of Flax Pond are clearly heterotrophic, as P: R ratios fall below zero during half the months of the year, yet the salt marsh flats appear to produce as much oxygen as they consume. This trend toward heterotrophy in the benthic communities represents some larger processes occurring in Flax Pond. In addition to oxygen, the waters entering Flax Pond from Long Island Sound also carry dissolved nutrients. Although not included in our analysis, these nutrients surely play a role in the biological dynamics of Flax Pond. If we hypothetically remove the waters of Long Island Sound from Flax Pond, we can infer how the biota of the pond would be drastically different. The exchanges of these two ecosystems have an effect on each system, but this effect is certainly more significant in Flax Pond. In many ways, the Flax Pond ecosystem is dependent on the delivery of oxygen, exchange of nutrients, and the removal of materials that Long Island Sound tide waters provide.

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