Measurement of in Situ Eelgrass Community Metabolism in Standing and Flowing Waters: Methods and Models

William James Seufzer

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MEASUREMENT OF IN SITU EELGRASS COMMUNITY METABOLISM IN STANDING AND FLOWING WATERS; METHODS & MODELS.

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

by
William J. Seufzer
1994
This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

William J. Seufzer

Approved, October 1994

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ABSTRACT

Five methods were investigated for measuring *Zostera marina* community metabolic rates. Metabolism measurements were based on dissolved oxygen (DO) exchange. The five methods were accomplished under enclosing hemispherical domes and with an array of DO sensors in the water column. Slack, diurnal curve, and two upstream-downstream methods (Eulerian and Lagrangian) were accomplished with the array of DO probes. Data collected from the array were used in computational models to evaluate each of the four open-water methods. Parameters used to compare the methods included gross production, community respiration, and production to respiration ratio (P:R). Comparison of the dome method to the open-water slack method showed each method estimating gross daily production from 8.0 - 13.7 gmO$_2$ m$^{-2}$ day$^{-1}$, community respiration from 7.4 to 11.0 gm O$_2$ m$^{-2}$ day$^{-1}$, and production to respiration ratio from 0.9 to 1.5. Results were numerically similar but lack of sufficient replication did not allow the differences or similarities to be shown as statistically significant. The diurnal, Eulerian, and Lagrangian methods accounted for moving water. In estimating net apparent production vs. water velocity, two of the methods (diurnal and Eulerian) showed a positive relationship but the results at higher velocities could not be shown as different from rates published in the literature studies using small chambers and domes. This study suggests that a slack water method with improved measures of reaeration could be used to replace the dome method and be applied to long-term monitoring. A qualitative relationship between water velocity and production estimates was shown in a comparison of slack (little to no water velocity) and diurnal (higher water velocities) methods. This study was not able to show a statistically significant relationship between water flow and production estimates.
MEASUREMENT OF IN SITU EELGRASS COMMUNITY METABOLISM IN STANDING AND FLOWING WATERS; METHODS AND MODELS.
INTRODUCTION

Ecosystems are collections of many types of behaviors carried out from molecular levels to the level of organisms. Each individual behavior plays a role, combines with other behaviors, and collectively they emerge as properties which we observe and use to classify and characterize different ecosystems. Some behaviors collect to form coral reefs, while similar and other behaviors collect in different ways to form rain forests, seagrass meadows, salt marshes, farmland, and cities. But this is not the end. Ecosystems neighbor each other and their behaviors collect and emerge as the biosphere which we call earth. Going further one could include the solar system, galaxies, and the universe.

Some of the observable properties of an ecosystem are the species of plants and animals and their population sizes. Looking closer, one might examine the pathways and magnitudes of energy transfer within systems as a means to compare the differences and similarities between ecosystems. Biomass and nutrient concentrations change, sometimes with pattern, as a result of these pathways and energy transfers. In an aquatic ecosystem behaviors of the plants, animals, the air-water interface, and the benthic-water interface cause the chemical makeup of the water to change. A pattern emerges such that during daylight hours the concentration of dissolved oxygen (DO) in the surrounding water column increases as plants and phytoplankton photosynthesize. During dark periods the DO concentration decreases as the entire community respires. This pattern is complicated by respiration of the entire community during light and dark periods, by exchange of oxygen with the atmosphere, and by use of oxygen in chemical reactions within the water column and benthic layer. If DO concentrations in the water are measured over time, the magnitude and timing of this signal can be used to characterize the metabolic activity within the community.
Odum & Wilson (1962) state that "To carry out research, evaluate fertility, appraise pollution, predict biological events, manage production, develop resource yields, and farm the vast shallow oceans, one must be able to assay day by day the total photosynthesis and respiratory consumption of these ecosystems." Their paper continues with refinements of using the diurnal curve method to estimate gross production and community respiration in several Texas bays in a variety of aquatic communities. (The diurnal curve method is presented in Odum & Hoskin (1958) and summarized later in this paper.) Odum & Wilson also suggest that metabolic studies leading to estimates of gross production and community respiration can be used to “... compute rates of turnover of chemical cycles, rates of uptake of radioactive substances, productivities, potentials for increased yields of marine products, and metabolic conditions...”. The following examples from the literature use metabolic measurements for estimation or characterization of biological activity.

Sargent & Austin (1949) used measurements of oxygen and phosphate as indicators of organic productivity of an atoll system. They show that reef systems are self-supporting by absorbing inorganic nutrients instead of filtering organic matter from the passing waters. Oxygen consumption was used to estimate a maximum growth rate of 1.4 cm year\(^{-1}\) for the reef.

Odum (1960) states that "... the relative amounts of inflow and outgo of organic matter and raw materials control the nature of metabolism. Imports of organic matter favor respiration whereas imports of regenerated inorganic raw materials stimulate photosynthesis." Odum compared diurnal curves of DO from polluted waters (rich in organic materials) to curves from unpolluted waters (rich in nutrients) to illustrate differences in the diurnal curves. The diurnal signal from unpolluted water shows a much higher peak in DO concentrations, and correspondingly higher community production, than the relatively flat (respiration dominated) signal from polluted waters. In a later study Odum (1963) used this comparison method to ascertain the effects of dredging near a turtle
grass community. The study showed decreased productivity by the grass beds during and after the dredging, but apparent complete recovery by the system in the following year.

Several other methods have been developed for measuring community metabolism. Vollenweider (1974) describes methods for measuring production for phytoplankton, macrophytes, and periphyton by using oxygen (O₂) exchange, carbon dioxide (CO₂) exchange, and ¹⁴C - carbon isotope tracer. Techniques to carry out these methods include light and dark bottles, running water, and standing water. A review of methods applied to macrophytes is summarized in Kemp et al. (1986). Methods include plant biomass harvest, elongation of marked leaves, exchange of metabolic gases (O₂ and CO₂) in bottles and under bell jars, and ¹⁴C radio isotope uptake. Kemp et al. compared “six methods for measuring primary production in submersed macrophytes to test for possible inherent shortcomings in the oxygen-exchange techniques.” They conclude that all gas exchange methods, each with individual strengths and weaknesses, are potentially useful for measuring productivity depending on the objectives of the study.

In the study of production rates of *Zostera marina*, several gas exchange methods have been used including: leaf segment studies, whole plant bottle incubations, and *in situ* studies using large hemispherical domes (Marsh et al., 1986; Murray, 1983; Wetzel, 1983). These methods are variants of the classic light-dark bottle method having different temporal and spatial scales. Leaf segment studies measure the exchange of O₂ from excised 1-2 cm segments of leaf placed in a small temperature and light controlled chamber. Marsh *et al.* (1986) performed leaf segment experiments to study the effects of temperature on photosynthesis and respiration in *Z. marina*. Optimum temperature for the photosynthetic maximum was 25 °C and respiration was shown to increase with temperature. Studies were performed at 5 °C intervals from 0 to 35 °C. Whole plant bottle incubations using BOD bottles measure metabolic rates of the entire plant with or without the roots and rhizome attached. Measurements at this scale are useful to relate metabolic
rates to the biomass of the plant. At a still larger scale, dome studies have been used to measure seagrass community metabolism rates. For this method an area of seagrass in the field is enclosed under a hemispherical dome. DO changes over time include contributions made by the entire community within the dome. BOD bottle incubations of epiphytes and water column can be used to estimate their contribution to the community metabolism signal. By subtracting the contributions made by the epiphytes and water column, an estimate can be made for the contribution due to the seagrass.

But techniques that isolate the organism or community by containment are questionable in situations where water velocity may have an effect on production rates. Odum (1956) compared production rates obtained with an upstream-downstream diurnal curve method to published data in various aquatic ecosystems taken with enclosed systems. Production rates in moving water were higher. Conover (1968) was able to show this relationship for Z. marina. Hourly current readings were averaged over complete neap to spring tidal cycles from several study sites. Standing crop was also measured and plotted against the water velocity regime. A positive relationship was indicated for velocities up to 1 knot (51 cm sec$^{-1}$) after which a negative relationship was indicated. This type of relationship has also been shown for other species such as Ruppia maritima and Thalassia testudinum. Nixon & Oviatt (1972), in a study comparing a Z. marina community in a stagnant pond to a Z. marina community in flowing water found higher production rates for the community in the flowing water. In their discussion the authors admit that there were differences in standing stock and community structure that may have accounted for the differences between the two communities. But in the case of the flowing water community regression lines are presented that show a relationship between apparent oxygen release (production) and uptake (respiration) and water velocity. Fonseca and Kenworthy (1987) presented evidence from flume experiments that growth rates for Z. marina are affected by water velocity. A positive relationship was shown between specific production and water velocity. Several effects of water velocity on seagrass production are mentioned, which
include: reduction of the diffusive boundary layer and enhancement of nutrient uptake; complete flushing of the meadow with surrounding water to help mediate CO$_2$ concentrations; changes in the canopy (leaf bending for example) influencing “diffusion boundary layer thickness, turbulence, discharge, momentum and temperature flux and light quality within the canopy”; and movement (swaying) of the plant within the flow.

Other points to consider in terms of water velocity and its relation to seagrasses are the effects of current on community structure and the range of water velocities that _Z. marina_ are known to experience. Fonseca et al. (1983) related dynamics of flowing water to the development of _Z. marina_ habitat. Height to length ratios of meadows were positively correlated with current regime and were suggested as a means to classify different seagrass meadows. The authors also documented the existence of _Z. marina_ in water velocities as high as 120-150 cm sec$^{-1}$. Since Nixon and Oviatt (1972) studied a _Z. marina_ community in a pond, and Conover (1968) documents velocity regimes up to ca. 75 cm sec$^{-1}$, it is clear that _Z. marina_ communities can exist in a large range of water velocity regimes. However, to date most studies on metabolic characteristics of _Z. marina_ communities have been done in closed systems.

One assumption made in metabolic studies in closed systems is that metabolic rates are not a function of water velocity. While containment simplifies data collection and calculation of metabolic rates, effects of water velocity and changes in ambient nutrient levels are filtered out by the container. Kemp and Boynton (1980) compared production and respiration rates measured in closed systems (bottles and chambers) and open water. They estimated production and respiration rates for open water measurements 1.5 to 4 times greater than that of closed system measurements. The authors suggest that the differences “may be due to artificial decoupling of the experimental systems from major pathways of nutrient flux”.

6
Flowing water can have an effect on several aspects of a seagrass community but this study focuses on the effects of water velocity on metabolic rates. The increase in metabolic rates, photosynthesis and respiration, as a result of water flow has already been shown for cnidarians on coral reefs (Patterson et al., 1991), kelp (Wheeler, 1980), periphyton (McIntire, 1966; Riber & Wetzel, 1987), and freshwater microphytes (Whitford & Schumacher, 1964). While Riber & Wetzel (1987) measured phosphorus instead of metabolic gas transfer, the paper provides quantitative techniques and visual demonstrations of the principles involved in boundary layer transfer. The relationship between velocity and metabolic rates can be explained in how water velocity alters the thickness of the boundary layer between water and the exchange surface of the organism. Fick’s first law (Okubo, 1980) in equation form is:

\[ F_x = -D \frac{\partial C}{\partial x} \]  

where \( F_x \) is the flux of the dissolved material (nutrient or metabolic gas) from the surrounding medium to the exchange surface (mass time\(^{-1}\)), \( D \) is the diffusivity of the dissolved material (length\(^2\) time\(^{-1}\)), \( \frac{\partial C}{\partial x} \) is the concentration (mass length\(^{-3}\)) gradient of dissolved material over the boundary layer of length \( x \) (length), where \( x \) is measured normal to the surface.

At low velocities the diffusive boundary layer (\( \partial x \)) is thicker than at high velocities. Wheeler (1980) showed theoretical curves for boundary layer thickness vs. water velocity. A thicker boundary layer (larger \( \partial x \)) decreases the magnitude of the concentration gradient (\( \frac{\partial C}{\partial x} \)) and decreases the diffusion rate \( F_x \). This would restrict the organism's metabolic rate by limiting the transport of \( O_2, CO_2 \), and nutrients to and from the water column. Higher velocity flows lead to thinner diffusive boundary layers and higher diffusion rates.

A positive relationship between water velocity, metabolic rates, growth rates, and standing crop has been shown for \( Z. marina \) and is most likely explained by diffusive
boundary layer dynamics. Ignoring this relationship could lead to underestimates of short- 
term and annual gross production and community respiration in Z. marina communities.
Methods exist for measuring community metabolism in moving waters and need to be 
applied to Z. marina communities.

This thesis investigates five methods for measuring Z. marina community 
metabolism rates, based on oxygen exchange, in standing and flowing waters. Two 
methods were compared for measuring metabolic rates in slack water: 1) hemispherical 
domes, and 2) open-water slack. The first objective of this study was to compare the dome 
method to the open-water slack method for possible differences between closed system and 
open-water measurements with little or no current. Three methods were compared for 
measuring metabolic rates in flowing water: 1) open-water diurnal, 2) 
upstream/downstream Eulerian, 3) upstream/downstream Lagrangian. The Eulerian 
method used an instantaneous measurement of the DO gradient across the seagrass bed in 
the direction of the water flow. The Lagrangian method considered travel time for a water 
parcel to traverse the seagrass bed from an upstream probe to a downstream probe. The 
second objective was to compare three open-water methods for their ability to measure 
metabolic rates vs. water velocity in a seagrass community. The combination of slack 
water methods and flowing water methods addresses the relationship between water 
velocity and metabolic rates in flowing waters and in near-zero flow (slack) conditions.
STUDY SITE

The study site was near Goodwin Island, VA near the mouth of the York River. 37° 12’ N 76° 23’ W which is part of NOAA’s National Estuarine Research Reserves (NERR) (Figure 1). This site was chosen for it’s proximity to VIMS (5 miles east of VIMS) and for possible collaboration with other studies conducted in the area. The study was conducted on the south side of the island near the middle of an established and stable seagrass community. As one moves towards the shore the community structure changes from primarily Z. marina, to Z. marina mixed with Ruppia maritima, to primarily R. maritima near shore. Moving away from the shore the community thins with increasing water depth as one approaches a navigable channel.

All data collection was accomplished over the same eelgrass bed and within the same time frame, May 11 to June 8, 1993. Use of the same location and time frame eliminated the possibility that different rates determined by different methods were due to differences in community structure, location, or seasonal variation. Since only 4 channels for DO measurements were available, the dome study was scheduled for the week following completion of the array collection. The time interval of one week is assumed negligible relative to differences in the grass bed that would occur on a seasonal scale.

All measurements and comparisons were made at the community level (i.e., additional measurements were not made to partition the effects of phytoplankton, epiphytes, or the sediment). The studies were conducted during the spring (water temperature ca. 20 °C) when about 80% of the community production is due to seagrass and epiphytes, and the biomass of epiphytes is low (Murray & Wetzel, 1987).
FIGURE 1

Map of study site. The study site, marked with an O, was on the south side of Goodwin Islands in an established and stable seagrass community.
METHODS & MODELS

Five methods were used to estimate community metabolic rates based on dissolved oxygen (DO) exchange. The methods were:

1) Dome,
2) Open-water slack,
3) Open-water diurnal,
4) Upstream/downstream Eulerian,
5) Upstream/downstream Lagrangian.

The dome and open-water slack methods were used to estimate metabolic rates in stagnant, or near stagnant, water. The remaining three methods; open-water diurnal, upstream/downstream Eulerian, and upstream/downstream Lagrangian, were used to estimate metabolic rates in moving water.

Data collection for the open-water and upstream/downstream methods was accomplished simultaneously. Collection for the dome method was done separately but over the same seagrass community. Vertical temperature data were also collected to test for stratification. All data were transferred into Matlab® (numerical analysis and data visualization software by The Mathworks Inc.) for analysis.

For each method a computational model was developed in Matlab® to derive daily production rate estimates. Each model used the same data (only the dome method had a unique data set) but employed a set of rules to produce daily production rate curves for each method. Another algorithm was then used to estimate net daily production, maximum production rate, net respiration, maximum respiration, average respiration, gross production, community respiration, and production to respiration (P:R) ratio. The estimates of metabolic rates from each model were used to compare the models. The flowing water models (3, 4 & 5 above) also tracked water velocity for each production rate.
calculation. Ranges of velocities were grouped and estimates of metabolic rates were then computed for each range. Metabolic rate estimates that do not consider the effects of water velocity can then be compared to estimates that consider water velocity.

**Data Collection**

Two methods of data collection were necessary to provide the data needed for the five methods and models. The difference between the two methods is in how DO measurements are collected (where the probes are placed). The first collection method involved placing replicate acrylic domes over areas of seagrass and monitoring DO in each dome. The use of domes is discussed in detail by Wetzel (1983). Three replicate domes were anticipated, however one was damaged beyond repair during transit to the field site. In addition to measuring DO in the two domes, two probes were placed 30 cm above the sediment, within the seagrass canopy, to measure ambient DO and temperature. The second collection method involved four dissolved oxygen sensors deployed in the open water and configured in an array. Figure 2 illustrates both methods: a) Dome and b) Open water array.

A third collection method was employed between the dome and field array studies. The open-water methods assume that the water column is vertically well mixed. The four DO probes, with temperature sensors, were deployed in a vertical array to determine if stratification occurs. For this, the probes were placed on a pole to sample at 10, 20, 30, and 40 cm above the sediment surface. Since salinity data could not be obtained at this spatial resolution, stratification was indicated by temperature and not by density.

Table 1 summarizes data collection parameters, units, rates, sensor position, instrumentation, and logging devices. For the dome method, only DO and temperature were measured inside the domes and in the open water near the domes. Depth, water velocity, and barometric pressure were not logged (they are unnecessary for estimating
production rates within domes). The array method makes use of all measured parameters.
Measurement of water velocity, light, salinity, and depth in the middle of the array
assumes that these parameters are uniform across the entire array.
Figure 2

Arrangement of equipment used for Dome and Open Water studies. One dome (a) is shown in side view (two replicate domes were used) along with one probe (two replicates) to measure water column DO and Temperature. Open water arrangement (b) is shown in plan view.
### TABLE 1

#### DATA COLLECTION SUMMARY

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>UNIT</th>
<th>SAMPLE INTERVAL</th>
<th>HEIGHT (above sediment)</th>
<th>DEVICE</th>
</tr>
</thead>
<tbody>
<tr>
<td>DO</td>
<td>mg/L</td>
<td>5 min.</td>
<td>30 cm</td>
<td>Endeco/Tattleale</td>
</tr>
<tr>
<td>Temperature **</td>
<td>°C</td>
<td>5 min.</td>
<td>30 cm</td>
<td>Endeco/Tattleale</td>
</tr>
<tr>
<td>Water Velocity</td>
<td>cm sec⁻¹</td>
<td>5 min.</td>
<td>30 cm</td>
<td>Marsh-McBirney w/ Tattleale</td>
</tr>
<tr>
<td>Submarine Light *</td>
<td>Einsteins m⁻²</td>
<td>5 min.</td>
<td>30 &amp; 50 cm</td>
<td>LICOR</td>
</tr>
<tr>
<td>Salinity **</td>
<td>psu</td>
<td>15 min.</td>
<td>10 cm</td>
<td>Hydrolab</td>
</tr>
<tr>
<td>Depth</td>
<td>meters</td>
<td>15 min.</td>
<td>10 cm</td>
<td>Hydrolab</td>
</tr>
<tr>
<td>Barometric pressure **</td>
<td>in Hg</td>
<td>60 min.</td>
<td>N/A</td>
<td>Newport News Airport +++</td>
</tr>
</tbody>
</table>

* Logged as integrated light over 5 minute period and converted to µE m⁻² s⁻¹.
** Needed by Endeco software computation of DO concentration.
*** Technician readings from mercury tube barometer. Logged in inches, converted to mm.

**Dissolved Oxygen and Temperature**

All DO and temperature measurements were taken with an Endeco/YSI Type 1125 (referred to here as T1125), 4 channel pulsed DO measurement system. Each probe has a pulsed polarographic (Clark type) oxygen sensor and thermister for temperature. A pulsed system was chosen as pulsed systems do not require stirring and are insensitive to water velocity (this was verified in a flume study during current meter calibrations). Calibration of the DO sensors was accomplished with Endeco's extensive four-point calibration (Endeco Type 1125 Pulsed DO System Hardware and Software manual) before and after deployment. Field deployment details are given in Appendix A.
Water Velocity

Water velocity was measured with a Marsh-McBirney model 721 electromagnetic current meter. An electronic interface was designed so that a Tattletale 5F-LCD computer could turn the current meter on (1 minute allowed for warm-up) and off and monitor its recorder outputs. Deployment details are given in Appendix A.

Logging of water velocity readings was simultaneous with DO and temperature data since the Tattletale computer logged water velocity, DO, and temperature. The sensor was cleaned daily to eliminate the effects of fouling.

Submarine Light

Integrated light readings were taken using LICOR 4π light sensors and logged by a LICOR LI-1000 datalogger. Sensors were cleaned daily to eliminate the effects of fouling. Calibration of light sensors is performed periodically by the manufacturer.

Salinity and Depth

Temperature, salinity (computed from conductivity), pH, and water depth were measured using a Hydrolab Datasonde II. The logging interval for the Hydrolab was set to 15 minutes while most other data were collected at 5 minute intervals. Depth and salinity are the only measurements from the Hydrolab required for the various models. Changes in depth and salinity are not fast enough to require a 5 minute sampling rate; 15 minutes was assumed adequate for these parameters.

The depth of measurement (relative to the bottom) was determined by a number of factors and constraints. It was assumed that the water column would be well mixed and vertically homogenous at all times. Placement of the Hydrolab probes at 10 cm above the sediment, as opposed to 30 cm, was constrained by the dimensions of the unit. This has no effect on depth measurements since the height of the probe is simply added to the probes.
reading to obtain true depth. Salinity readings are used in calculating saturation DO levels and for salinity compensation in DO readings by the Endeco model 1125. It was assumed that salinity gradients over a distance of 20 cm would not be large enough to cause significant errors.

The Datasonde is equipped with a datalogger and computer interface. As part of the calibration procedures, the instrument was programmed with starting time, ending time, and interval of collection.

Calibration for conductivity was accomplished with 0.2N KCl (24.82 mS cm\(^{-1}\)). Standard pH buffers of 7.00 and 9.00 were used to calibrate pH. Depth was calibrated to 0.0 m at sea level. Temperature does not require calibration on the Hydrolab Datasonde II.

**Barometric Pressure**

Barometric pressure was recorded at Newport News/Williamsburg International airport (8.5 miles southwest of the study site) at hourly intervals by weather station personnel. Barometric pressure differences within 8.5 miles are assumed negligible. While the passage of storms fronts can cause large changes in barometric pressure in a relatively short time, the hourly data was the best available. Linear interpolation (provided by Matlab\(^{®}\)) was used to obtain measurements between hourly intervals. Errors introduced by interpolation were assumed small.

**Reaeration Calculations**

Reaeration is the diffusive flux of oxygen across the air-water interface. Estimating this flux is necessary as a correction for open-water methods. Odum (1956) provided a method for estimating reaeration from rate change of oxygen curves. Copeland & Duffer (1964) used a plastic dome method to measure diffusive flux. They compared their method to Odum’s and found general agreement between them in stream studies. In standing water, they indicated that Odum’s method overestimates reaeration.
The study by Nixon & Oviatt (1972), comparing metabolism rates of pond and stream *Z. marina* communities, used the dome method to measure reaeration in the pond study and an empirical method by Edwards & Owens (1964) in the stream. For this study it was assumed that Odum’s method would not apply where water velocity and depth were variable on the time scale of hours, unlike a stream. The dome method was not amenable to automated sampling and was considered impractical for this study. The method of Edwards & Owens (1964) (equation 2) was chosen since the empirical relation considered water velocity, water depth, could be applied to open-water data sets, and would make results of this study comparable to those of Nixon & Oviatt (1972) which studied similar communities. The equation (Edwards & Owens, 1964) used for reaeration is:

\[ F = [9.41 \times V^{0.67} \times H^{-1.85}] \times (C_s - C) / 24 \]  

where:

- \( F \) = the diffusive flux in mg liter\(^{-1}\) hour\(^{-1}\),
- \( V \) = the water velocity in ft sec\(^{-1}\)  
  (Conversions are made in the software to convert metric units to English.)
- \( H \) = the water depth in ft,
- \( C_s \) = the saturation concentration of DO in mg liter\(^{-1}\),
- \( C \) = the water column concentration of DO in mg liter\(^{-1}\), and
- 24 converts the daily rate to an hourly rate.

**Dome Method and Model**

For this method one meter diameter, 260 liter acrylic domes were placed over the seagrass community. Each dome is equipped with a 10 cm vertical flange which was pushed into the sediment to seal the dome and secure it in place. A submersible water pump circulated water within the dome to insure that the water was well mixed. Endeco/YSI DO probes were installed through the dome (see Figure 2).
An advantage of the dome method is that the hemispherical domes enclose the intact seagrass community and reduce the data collection requirements; i.e., physical factors such as reaeration and water velocity can be ignored. But domes enclose the community and possibly modify the community response (Kemp & Boynton, 1980). Also, if community metabolism is related to water velocity, the dome inhibits this effect. The mathematical model used to calculate exchange in domes was:

\[ P = (DO_t - DO_{t-5}) \times \frac{60}{\Delta t} \times \frac{\text{Vol}}{\text{Area}} \]  

where:
- \( DO \) = dissolved oxygen measured in mg liter\(^{-1}\),
- \( \Delta t \) = the time between \( DO_t \) and \( DO_{t-5} \) in minutes (5 minutes),
- \( \text{Vol} \) = the volume of the dome in liters,
- \( \text{Area} \) = the area of seagrass community covered by the dome in meters\(^2\), and
- \( P \) = the net production rate in mg O\(_2\) m\(^{-2}\) hr\(^{-1}\).

The Matlab routines that perform dome model calculations are summarized and given in Appendix B.

**Open Water Slack Method and Model**

Kinsey (1978) used a slack water method to estimate productivity and calcification rates on coral reefs. Over a tidal cycle there are periods of near zero water velocity. Due to tidal progression, the slack water period occurs at different times of the day advancing at about 12 minutes per cycle. If sampling is accomplished over half of a lunar cycle (i.e., full to new moon) then a set of slack periods can be combined to create an aggregate "slack day". Ideally all slack intervals are grouped by hour of day into a 24 hour period with a slack interval every 12 minutes. This assumes that day to day variability in light, temperature, and other factors affecting production, are small.

Since the slack water method will be compared directly with dome results, it is assumed that the near slack conditions in the water column are similar to the conditions
within the circulated domes. It is also assumed that since the water mass travels very slowly, essentially the same water mass is being sampled over the time period. As with all open water methods, it is assumed that the water column is well mixed.

The computational model uses each DO probe independently allowing four replicate measurements of community metabolism. A second model averages the DO readings from all four probes at each interval to filter out the spatial variability within the seagrass bed. At a maximum velocity of 0.5 cm sec\(^{-1}\) the water will move 3.0 meters over a 10 minute sampling period. Production calculations are made from the data set where the velocity of the water column is less than 0.5 cm sec\(^{-1}\) and the change in velocity over a 10 minute period is less than 0.1 cm sec\(^{-1}\). These conditions indicate a slow and constant current. Selection of these criteria is subjective. A velocity less than 0.5 cm sec\(^{-1}\) is considered as slack for all models in this study. The 10 minute period and 0.1 cm sec\(^{-1}\) criteria were manipulated until over 100 data points were available for production rate calculations. When these criteria are met, DO readings are taken from a probe at the beginning and end of the 10 minute period. Production rates are calculated as follows:

\[
P = (DO_{t+5} - DO_{t-5}) \times \frac{60}{\Delta t} \times \text{Depth} \times 1000
\]

where:
- \(DO\) = dissolved oxygen measured in mg liter\(^{-1}\) at times \(t+5\) and \(t-5\) minutes,
- \(\Delta t = 10\) minutes,
- \(\text{Depth}\) = water column depth in meters,
- \(1000\) = a conversion from liters to m\(^3\), and
- \(P\) = the net production rate in mg O\(_2\) m\(^{-2}\) hr\(^{-1}\).

The Matlab routines that perform slack water model calculations are summarized and given in Appendix C.
Open Water Diurnal Method and Model

The open water diurnal method makes use of one probe from the array and can be used in slack and moving water. Typically, DO measurements are taken at pre-selected intervals over at least a 24 hour period. Odum & Hoskin (1958) described ways to estimate a suite of community metabolism parameters from these measurements. An assumption of this method is that the history of a parcel of water approaching the monitoring station has had a similar history to the parcel leaving the station. Using Odum & Hoskins (1958) sampling interval of 3 hours, it must be assumed that moving water maintains its speed and direction. This assumption cannot be made in a seagrass bed so shorter intervals are used. As with all open water methods, it is assumed that the water column is well mixed.

Here the method is modified to use shorter sampling intervals and to select sampling periods based on the physical environment. As for the slack water model, criteria were established for water velocity and for velocity changes over the sampling interval. Changes in DO were measured with individual probes allowing 4 replicates at selected time intervals. A fifth “replicate” was provided by averaging DO measurements from the 4 probes.

Production calculations are made from the data set where the velocity of the water column is greater than 0.5 cm sec\(^{-1}\) and the change in velocity over a 10 minute period is less than 0.15 cm sec\(^{-1}\) (i.e., the maximum and minimum velocities for the period differ by no more than 0.15 cm sec\(^{-1}\)). As for the slack water model, selection of these criteria is subjective. A velocity criteria greater than 0.5 cm sec\(^{-1}\) ensures water movement and separates this model from the slack model. Different criteria (time periods and velocity ranges) were attempted until over 100 data points where available for production rate.
calculation. When these criteria are met, DO readings are taken from a probe at the beginning and end of the 10 minute period. Production rates are calculated as follows:

\[
P = \left[ (\text{DO}_{t+5} - \text{DO}_{t-5}) \times \frac{60}{\Delta t} \times \text{Depth} \times 1000 \right] - \text{Reaeration}
\]

where:

- \( \text{DO} \) = dissolved oxygen measured in mg liter\(^{-1}\) at times \( t+5 \) and \( t-5 \) minutes.
- \( \Delta t = 10 \) minutes,
- Depth = water column depth in meters,
- 1000 = a conversion from liters to m\(^3\),
- Reaeration = diffusive flux correction (described earlier), and
- \( P \) = the net production rate in mg O\(_2\) m\(^2\) hr\(^{-1}\).

The Matlab routines that perform the open-water diurnal model are summarized and given in Appendix D.

The open-water diurnal model is the first in this study to consider moving water. In addition to the calculations outlined above, calculations are also made to generate production vs. water velocity estimates. The steps above are the same except that the water velocity criteria is changed to use a range of velocities. That is, metabolic parameters were computed for velocity ranges of 0.0 to 0.5 cm sec\(^{-1}\), 0.5 to 0.85 cm sec\(^{-1}\), 0.85 to 1.2 cm sec\(^{-1}\), and 1.2 to 8.0 cm sec\(^{-1}\).

**Upstream/Downstream Eulerian Method and Model**

The upstream-downstream Eulerian method makes use of the array geometry and is based on Sargent & Austin (1949). Dissolved oxygen measurements are taken from a pair of probes at the same time, and the resulting difference is used to calculate a production rate. Three assumptions are necessary. The first assumption is that the water velocity has been relatively constant. If the flow field changes direction the separation distance between the probes has changed. If the water velocity is not constant the residence time of the water over the bed is not constant and calculation errors are introduced. The second assumption
is that the production of oxygen along any radial path within the bed is uniform (i.e., the entire bed is uniform). If the current direction changes between two valid measurement points a different path is traversed across the bed. It is assumed that the production rates along each path are similar. The third assumption is that the water column is well mixed.

The mathematical model used for this method set water velocity conditions required to support the first assumption. Uniformity of the sea grass bed was neither tested nor was any surrogate measurement (i.e., biomass estimates along diagonal transects) made. Evidence from the vertical array showed that there were periods when the water column would stratify. Stratification will be discussed later.

The mathematical implementation of this model uses water direction to determine which probes will be used as the upstream and downstream pair (in a flow towards the east, the west probe is assigned upstream, and the east probe is assigned downstream). Travel distance is based on the sine or cosine of the direction multiplied by the probe separation of 50 meters. This assumes that a dissolved oxygen gradient is traveling as a front, i.e., there is no lateral diffusion (Nixon & Oviatt, 1972). Further requirements of the model are that the water velocity be greater than 0.5 cm sec$^{-1}$ and that the change in velocity over a 20 minute period not exceed 0.4 cm sec$^{-1}$. As with the previous models these criteria are subjective and manipulated to capture, in this case, enough points to obtain a representative number of calculations for each hour (typically about 100 data points).
When these conditions are met the following equation is used to calculate a production rate:

\[ P = [(DO_{downstream} - DO_{upstream}) \times (60/\Delta t) \times \text{Depth} \times 1000] - \text{Reaeration} \]  \hspace{1cm} (6)

where:
- \( DO \) = measured in mg liter\(^{-1}\),
- \( \Delta t \) = the residence time of the water in minutes (travel distance/average velocity),
- \( \text{Depth} \) = average depth in meters over the interval,
- 1000 = a conversion from liters to m\(^3\),
- \( \text{Reaeration} \) = the diffusive flux correction, and
- \( P \) = the net production rate in mg O\(_2\) m\(^{-2}\) hr\(^{-1}\).

The Matlab® routines that perform the Eulerian model are summarized and given in Appendix E.

Calculations are also made to generate production vs. water velocity estimates. Metabolic parameters were computed for velocity ranges of 0.0 to 0.5 cm sec\(^{-1}\), 0.5 to 0.85 cm sec\(^{-1}\), 0.85 to 1.2 cm sec\(^{-1}\), and 1.2 to 8.0 cm sec\(^{-1}\).

**Upstream/DownStream Lagrangian Method and Model**

The upstream-downstream Lagrangian method makes use of the array geometry and is based on Odum (1956). This method was also used by Nixon & Oviatt (1972) as their flowing water method. DO measurements from a pair of probes are taken at different times based on the travel time of water from probe to probe. No assumptions are made about the constancy of the water velocity except for direction, and it is assumed that the water column is vertically well mixed at any velocity.

The computational model uses current direction to determine upstream and downstream probes. Travel distance is calculated as with the Eulerian model. At the beginning of a sampling interval the upstream probe dissolved oxygen measurement is stored. Water velocity is then integrated into distance traveled to track a parcel of water.
from the upstream probe to the downstream probe. As the parcel travels, the direction of travel is not allowed to change by more than 30 degrees from the original direction. Use of the 30 degree criteria is subjective. To exclude velocities less than 0.5 cm sec\(^{-1}\), total travel time is not allowed to exceed 150 minutes for the 50 meter distance. If a deviation of more that 30 degrees is encountered the data is rejected. When the integrated travel distance is equal to, or slightly larger than, the calculated distance the dissolved oxygen reading is taken from the downstream probe. Calculation resumes by incrementing the start time and running the procedure over again. Under these conditions over 100 points can be used to generate production estimates using the following equation:

\[
P = \left[ (\text{DO}_{\text{downstream}} - \text{DO}_{\text{upstream}}) \times \left( \frac{60}{\Delta t} \right) \times \text{Depth} \times 1000 \right] - \text{Reaeration} \tag{7}
\]

where:

- \(\text{DO}\) = measured in mg liter\(^{-1}\),
- \(\Delta t\) = the residence time of the water in minutes (travel distance/average velocity),
- Depth = average depth in meters over the interval,
- 1000 = a conversion from liters to m\(^3\),
- Reaeration = the diffusive flux correction, and
- \(P\) = the net production rate in mg O\(_2\) m\(^2\) hr\(^{-1}\).

The Matlab® routines that perform the Lagrangian model are summarized and given in Appendix F.

Calculations are also made to generate production vs. velocity estimates. Metabolic parameters were computed for velocity ranges of 0.0 to 0.5 cm sec\(^{-1}\), 0.5 to 0.85 cm sec\(^{-1}\), 0.85 to 1.2 cm sec\(^{-1}\), and 1.2 to 8.0 cm sec\(^{-1}\).

**Calculation of Metabolic Parameters**

A routine was developed using Matlab® based on the methods of Odum & Hoskin (1958). It calculates maximum production, maximum respiration, mean dark respiration,
gross production, community respiration, and production to respiration ratio. These calculations are visually depicted in Figure 3.

Additionally net apparent production (NAP) is estimated two different ways for comparison to published rates. The first method for estimating NAP (NAP1) integrates all positive rates within the photoperiod and is based on Nixon & Oviatt (1972). The second method (NAP2) is based on Murray & Wetzel (1987). For NAP2 positive production rates between the hours of 10:00 and 14:00 are averaged and the resulting rate is integrated over 80% of the photoperiod. The Matlab® code that calculates NAP1 and NAP2 is part of the routine for estimating the other metabolic parameters and is given in Appendix G.

The five models call the Matlab® routine with four parameters. The first parameter is an abscissa (hour of the day vector) for the data (column vector), second is the pooled and averaged production rates in mgO₂ m⁻² hr⁻¹ (column vector, same size as abscissa), third is number of points averaged into the pooled and averaged rates (column vector), and the fourth is the interval of time in minutes used to group production rates (scalar). The calculations are performed and the results for each model entered into Table 2 (Results Section).

The Matlab® routine that calculates metabolic parameters is summarized and given in Appendix G.
FIGURE 3

Determination of metabolic parameters. Graphical representation of how metabolic parameters are determined from production rate curve. (Based on Odum and Hoskin (1958)).

Maximum Production Rate
Maximum Respiration Rate
Mean Dark Respiration Rate
Gross Production (gray area)
Community Respiration (striped area)
RESULTS

Over 100,000 data points were collected over the period of the study. The high sampling rate, afforded by automation, resulted in over 5000 sampling intervals of information collected for the dome and array methods.

The study was conducted during the spring to summer transition during which 80% of the seagrass community production is accounted for by $Z. \text{marina}$ (Murray & Wetzel, 1987). The average water temperature over the deployment period was 20 °C, and ranged from 17 °C to 24 °C. This range brackets the optimum growing temperature (20-22 °C) of $Z. \text{marina}$ (Wetzel & Penhale, 1983). Average water depth during the study was 0.8 meters and ranged from 0.4 to 1.4 meters. The average water velocity over the time period was 1.1 cm sec$^{-1}$ and ranged from 0.0 to 7.2 cm sec$^{-1}$. Salinity ranged from 12 to 15 psu with a mean of 13.3 psu.

Dome Measurements

The Endeco Type 1125 DO measuring system has an upper DO limit of 15 mg l$^{-1}$ but this upper value can change relative to each probes calibration. Probe 1 (corresponding to dome 1) was only able to record to about 12.5 mg l$^{-1}$, and probe 2 to just over 14 mg l$^{-1}$. Since the DO concentration in the domes exceeded these values a spline procedure was run to estimate missing values. This assumes that the spline curve mimics the behavior of the DO measurements during the sampling "black-out". Figure 4 shows DO concentrations over time in replicate domes 1 and 2.
FIGURE 4
Dissolved oxygen vs. time in replicate Domes 1 and 2. Circles are "real" data obtained from DO probe, solid line is splined "data" to fill in probe "blackouts" (explained in text). Data points are at 5 minute intervals. Gray bars on x-axis indicate photoperiod. Hour values over 24 are from second day of experiment (i.e., day 2 6:00 am = 30).
Data from dome 1 indicated DO concentrations going to values less than zero. Despite the rigorous 4-point calibration and "minimal drift" advertised by the manufacturer it is clear that there were calibration problems with this probe. While the calibration was not exact, the data and splined values were used since all calculations are based on differences in DO values.

Figure 5 shows the production rate calculations for each of the domes. A 24 hour period was chosen from the DO measurements from 1600 hrs of the first day to 1600 hours on the following day for these calculations. Note that the maximum production rate occurs before noon in each dome.
FIGURE 5

Net Production vs. time in replicate Domes 1 and 2. Production rates for each hour are pooled and averaged (solid line). Error bars indicate one standard error from mean; n=12 for each mean.
Figure 6 compares temperature and DO values within the domes to the surrounding environment. Temperature and DO values were averaged for each replicate pair to indicate potential differences between the two environments. The water in the domes appears to cool off slower than the open water during the evening hours but then warms up at about the same rate during the photoperiod. The mean temperature of the domes was 0.3 °C (but as much as 0.5 °C) warmer than that of the open water column. While not conclusive because of calibration problems with the probe in dome 1, it would appear that DO levels within the domes possibly go lower than in the open water column.
FIGURE 6

Averaged Temperatures and DO levels in the water column and domes (2 replicates each). Solid lines indicate open water probes, dotted lines indicate dome probes. Hour values over 24 are from second day of experiment (i.e., day 2 6:00 AM = 30).
Physical Environment

The following figures are included to show the environmental variability encountered over the 16 day array deployment. The aggregation of 16 days of results into a 24 period assumes that light and temperature were similar each day. That assumption, as shown here, is not entirely valid. Since water travels in all directions, it is clear that there is no constant upstream/downstream arrangement. Figure 7 shows mean and maximum water velocities encountered over the 16 day period. Figure 8 shows minimum, mean, and maximum light levels measured within the seagrass canopy (30 cm above sediment) and pooled by hour of the day. The values shown are the minimum, mean, and maximum encountered for each hour of the pooled data. The near-zero light periods during the daylight hours correspond to high tide and may also correspond to cloud cover and very turbid water. Water temperatures also change on a daily basis as is summarized in Figure 9. Reaeration estimates were also pooled from the 16 day array deployment and are shown in figure 10.
FIGURE 7

Represents the heterogeneity of current magnitude and direction. Mean and maximum velocities pooled by direction into 10 degree intervals for the entire 16 day experiment. Direction indicators line up with the DO probe array and are within 10 degrees of magnetic bearings.
FIGURE 8

Light measurements from 16 day period pooled by hour of day. Lines show minimum, mean, and maximum levels encountered during each one hour period.
Temperature measurements from 16 day period pooled by hour of day from all four probes. Lines show minimum, mean, and maximum temperatures encountered during each one hour period.
FIGURE 10

Reaeration estimates from 16 day period pooled by hour of day. Negative rates indicate $O_2$ leaving the water column. Positive rates indicate $O_2$ entering the water column. Mean is the average rate encountered over each 1 hour period. Estimates based on Edwards and Owens (1964).
The open water methods used in this study assume that the water column is vertically well mixed. To test this assumption, all four DO and temperature probes were installed on a pole to collect temperature at 10, 20, 30, and 40 cm from the sediment surface. Figure 11 shows a three day record (between the time of array and dome experiments) of the water column vertical temperature profile. The temperature readings from these probes have been found in the laboratory to agree with each other to within 0.02 °C. While the assumption of vertical mixing is mostly true, especially during evening hours, there are days when the water column may stratify. For example, temperatures were nearly equal through the first photoperiod and up to the second photoperiod. During the second photoperiod the water column stratified with warmer temperatures near the water surface. Some type of mixing event occurred later that day for a short period, after which the water re-stratified.
FIGURE 11

Temperatures measured at 10, 20, 30, and 40 cm from the sediment surface to test for stratification. Solid line is 10 cm, dotted line is 20 cm, dash-dot line is 30 cm, and dashed line is 40 cm from the sediment surface. Hour values over 24 are from second day of experiment (i.e., day 2 6:00 AM = 30). Gray bars indicate photoperiod.
Open Water Slack

Figures 12 a,b,c, and d illustrate results from the slack water model for each replicate probe. Figure 12e illustrates results from the slack water model where the difference in DO (for production rate calculations) was based on the averaged differences of the probes. For each analysis 16 days of results are combined into one 24 hour period based on hour of the day. Metabolic parameters for this model are summarized in Table 2.
Figures 12a, 12b, 12c, 12d, and 12e. Net Production vs. time for each probe and from averages of probe readings for the slack water model. Production rates for each hour are pooled and averaged (solid line). Error bars indicate one standard error from mean.
FIGURE 12E

Slack Probes Averaged

Net Production (mg O₂ m⁻² hr⁻¹)

Photoperiod

Time of day (hours)

0  2  4  6  8  10  12  14  16  18  20  22  24

-4000 -3000 -2000 -1000 0 1000 2000 3000 4000
Open Water Diurnal

Figures 13a, 13b, 13c, and 13d give results from the diurnal water model for each replicate probe. Figure 13e illustrates results from the diurnal water model where the difference in DO (for production rate calculations) was based on the averaged differences of the probes. For each analysis 16 days of results are combined into one 24 hour period based on hour of the day. Metabolic parameters for this model are summarized in Table 2.
Figures 13a, 13b, 13c, 13d, and 13e. Net Production vs. time for each probe and from averages of probe readings for the diurnal model. Production rates for each hour are pooled and averaged (solid line). Error bars indicate one standard error from mean.
FIGURE 13C

Diurnal Probe 3

FIGURE 13D

Diurnal Probe 4
FIGURE 13E

Diurnal Probes Averaged

Net Production (mg O$_2$ m$^{-2}$ hr$^{-1}$)

Photoperiod

Time of day (hours)
**Up/Downstream Eulerian**

Figure 14 gives results from the Eulerian model. 16 days of results are combined into one 24 hour period based on hour of the day. These results show no apparent production maximum as expected around 1000 hrs. Metabolic parameters for this model are summarized in Table 2.
FIGURE 14

Net Production vs. time for the Eulerian model. Production rates for each hour are pooled and averaged (solid line). Error bars indicate one standard error from mean.
Upstream/Downstream Lagrangian

Figure 15 gives the results obtained from the Lagrangian model. While the slack and diurnal methods had production rate maximums just before 1000 hrs, this method shows its maximum just after 1000 hrs (like the domes). Metabolic parameters for this model are summarized in Table 2.
FIGURE 15

Net Production vs. time for the Lagrangian model. Production rates for each hour are pooled and averaged (solid line). Error bars indicate one standard error from mean.
TABLE 2. Summary of maximum production rate, maximum respiration, mean dark respiration, NAP1, NAP2, gross production, community respiration, and production to respiration ratio (P:R). These values were computed by an algorithm based on Odum & Hoskins (1958), Nixon & Oviatt (1974), and Murray & Wetzel (1987).
### TABLE 2

Metabolic Parameters

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<th>Max Prod</th>
<th>Max Resp</th>
<th>Mean Dark R</th>
<th>NAP1 *</th>
<th>NAP2 **</th>
<th>Gross P</th>
<th>Comm R</th>
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</table>

* Integrated positive net production rates over photoperiod.
** Mean net production between 1000 hrs and 1400 hrs integrated over 80% of photo period.
**Net Apparent Production and Water Velocity**

The diurnal, Eulerian, and Lagrangian models were adapted to estimate NAP1 vs. water velocity. Velocity range selections are somewhat arbitrary but based on the number of data available for each range (an attempt was made to get nearly the same number of data points into each range). NAP estimations from each velocity group were then used to estimate NAP1 vs. velocity.

NAP vs. velocity is illustrated in Figure 16. The diurnal method shows a positive relationship up to the highest range where the rate decreases considerably. On the other hand the Eulerian method, except for the 0.5 to 0.85 cm sec\(^{-1}\) range, shows increasing production with increasing velocity. Because of selection criteria, the Lagrangian model makes no calculations in the 0.0 to 0.5 cm sec\(^{-1}\) range. The Lagrangian model shows decreasing NAP with velocity.
FIGURE 16

Net apparent production vs. velocity for the diurnal, Eulerian, and Lagrangian models. Each model was run and constrained by velocity range to produce a family of production curves (16 days pooled by hour into 24 hours). One production curve was computed for each velocity range. NAP1 was estimated from each production curve and is shown here. There is no replication available to calculate standard error.
DISCUSSION

The first objective of this study was to compare community metabolism rates measured in the open water column during near slack conditions to those measured using enclosed hemispherical domes. Statistical analysis was considered in this study but was not used due to lack of replication. Instead, rates for each method were compared to other methods and to rates obtained from the literature (Table 3).

**TABLE 3**

Summary of NAP estimates obtained from literature. Rates listed are maximum rates of $O_2$ exchange shown in each study. NAP1 and NAP2 were appended to each rate to differentiate the two ways NAP has been estimated. Dome rates based on photoperiod of 12.8 hours.

<table>
<thead>
<tr>
<th>NAPx</th>
<th>Method</th>
<th>Temperature</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(gm $O_2$ m$^{-2}$ day$^{-1}$)</td>
<td></td>
<td>Degrees C</td>
<td></td>
</tr>
<tr>
<td>7.1 NAP1</td>
<td>Small chamber</td>
<td>18 to 25</td>
<td>Kemp et. al., 1987</td>
</tr>
<tr>
<td>6.8 NAP2</td>
<td>Dome</td>
<td>10 to 20</td>
<td>Murray &amp; Wetzel, 1987</td>
</tr>
<tr>
<td>9.6 NAP2</td>
<td>Dome</td>
<td>18 to 26</td>
<td>Wetzel &amp; Pennale, 1983</td>
</tr>
<tr>
<td>2.9 NAP1</td>
<td>Open pond</td>
<td>24 to 28</td>
<td>Nixon &amp; Oviatt, 1972</td>
</tr>
<tr>
<td>3.6 NAP1</td>
<td>River</td>
<td>20 to 26</td>
<td>Nixon &amp; Oviatt, 1972</td>
</tr>
</tbody>
</table>

NAP is not dependent on estimates of, or assumptions made about, respiration rates and is therefore a simple rate to compare with other studies. Wetzel & Pennale (1983) and Murray & Wetzel (1987) used NAP2 (average net production rates between 1000 hrs and 1400 hrs integrated over 80% of the photoperiod) and suggested that the rates are maximum rates. In regards to dome studies, their rates may have overestimated production by a factor of 2. Table 2 shows estimates of NAP2 rates, on average, to be twice as large as NAP1 rates for this dome study. NAP1 integrates rates encountered over the entire photoperiod and should provide a more realistic estimate of NAP.
NAP1 estimates for a pond seagrass community in Nixon & Oviatt (1972) are less (2.9 gm O$_2$ m$^{-2}$ day$^{-1}$) than what is estimated here (4.0 to 9.0 gm O$_2$ m$^{-2}$ day$^{-1}$). The authors admit that their estimates may be low but do not offer a reason. The timing of their study was in early August at higher temperatures as compared to this study which was done in during the high growth season (May to June). Differences in season and community structure may account for differences between the Nixon & Oviatt study and this study.

Estimates of gross daily production are based on estimates of production and respiration and are used in this study as an “overall” measure to compare one method to another. Numerical ranges of gross daily production rates measured by the dome (8.3 to 10.0 gm O$_2$ m$^{-2}$ day$^{-1}$) and slack models (8.0 to 13.7 gm O$_2$ m$^{-2}$ day$^{-1}$) would indicate that the models predicted similar results (dome estimates are within the range of slack estimates). Gross production estimated by Slack3 seems abnormally high when compared to Slack1, Slack2, Slack4 and the Slack multi-probe model. There were no obvious problems suggested by the probes records of DO and time. Slack3 is higher than any dome or slack gross production but it’s estimate of NAP2 (7.1 gm O$_2$ m$^{-2}$ day$^{-1}$) was similar to NAP2 rates (6.8 to 9.6 gm O$_2$ m$^{-2}$ day$^{-1}$) listed in Table 3. Each replicate probe, including Slack3, seems to have measured the spatial variability within the seagrass meadow.

Estimates of gross production were similar but there were differences in estimates of other metabolic parameters. On average, maximum production rates encountered for the slack method were twice as high as those for the dome (1911 vs. 846 gm O$_2$ m$^{-2}$ hr$^{-1}$). Slack maximum respiration was slightly higher than the dome maximum respiration (1025 vs. 690 gm O$_2$ m$^{-2}$ hr$^{-1}$), but mean dark respiration estimates were similar (388 vs. 414 gm O$_2$ m$^{-2}$ hr$^{-1}$). If gross production and mean dark respiration were similar, then maximum production rates should also have been similar. Likewise, NAP1 should have been similar but NAP1 was slightly higher for slack than for dome (5.9 vs. 4.0 gm O$_2$ m$^{-2}$ day$^{-1}$).
While higher maximum production and higher NAP1 rates were encountered for the slack method, figure 12 reveals why gross production estimates were similar. Slack production rates between 1100 and 1400 hours drop considerably and go negative for three of the four probes. The domes (figure 5) do not show a similar drop in net production. If production rates had not dropped between 1100 and 1400 hours, NAP1 and gross production estimates would have been higher for slack. Explanation of the net production decrease is not obvious. Respiration rates of a system component would have to change for the time period between 1100 and 1400 hours but not when under a dome. Reaeration may have been a factor but was not computed for the slack method. Maximum reaeration rates (ca. 50 mg O$_2$ m$^{-2}$ hr$^{-1}$, Figure 10) encountered for the 16 day period were not large enough to account for this deficit. However, 1100 to 1400 hours was when reaeration rates were near or at a maximum. This would suggest the reaeration was underestimated in this study.

If reaeration was underestimated, and maximum production rates for the slack method indicate that higher NAP1 rates could be possible, then gross production estimates by the slack method may be underestimated in this study.

There were other environmental conditions which could have lead to differences in rates measured by the dome and slack methods. These were environmental variability, mean temperature, and dynamic range of DO. These are discussed in the following paragraphs.

While the dome method used an enclosed environment, the slack method was subjected to data collected in the open water column. The data for the dome model was collected over a single 24 hour period. Changes in DO within the dome appear smooth from sample to sample (Figure 4) and result in relatively small standard errors (Figure 5) when data over each 1 hour interval was pooled and averaged. In contrast, the slack model (Figure 12) data was pooled from a 16 day period into a 24 hour “slack day”. The day to day variability in water velocity, light, and temperature are shown in Figures 7, 8, and 9.
The variability in the physical environment lead to variability in the slack production measurements and to larger standard errors in the pooled data.

Figure 6 shows that the average temperature within the domes was about 0.5 degrees C higher than the ambient temperature in the water column. It also shows that DO levels within the dome were lower overnight than ambient DO levels. The temperature difference was larger during the evening and would allow respiration within the dome to occur at a slightly higher rate. Mean dark respiration rates encountered in the domes were slightly higher than those for the slack method (414 vs. 390 gm O$_2$ m$^{-2}$ hr$^{-1}$). While they were slightly higher it could not be shown that the difference was statistically significant. However, Murray and Wetzel (1987) indicate a significant correlation between temperature and respiration for seagrass communities.

During the course of the 16 day array experiment, DO levels in the water column did not exceed the dynamic range of the DO sensors. But in the dome experiment DO levels exceeded the dynamic range of the sensors at high and low concentrations. Placing a dome over a plot of seagrass causes the seagrass for that given area to be compressed into a smaller volume of water than it would occupy in the open environment. To compare numerically, the 260 liter domes cover 0.78 m$^2$ of area which allows about 330 liters of water for 1 m$^2$ of seagrass. Meanwhile in the open water environment, a 1 m$^2$ patch of seagrass has 1000 liters of water (1000 liters m$^{-2}$, assuming 1 meter water depth). DO concentrations will make larger excursions during the course of a day, but since volume is considered in production calculations, production rates are not over or underestimated.

While there were numerical differences in measurements between the dome and slack method, the differences were neither large enough nor consistent enough to conclude that the two methods gave different results. On average, gross daily production was slightly higher with the slack model but other parameters including mean dark respiration
and P:R all fell within the same range. Replication and a better estimate of reaeration would be needed to show that the slack method differed significantly from the dome method.

The second objective was to compare the abilities of the diurnal, Eulerian, and Lagrangian methods to explore net apparent production (NAP1) estimates and water velocity relationships. This is discussed qualitatively as flowing water methods are compared with the standing water methods, and quantitatively from estimates of NAP1 vs. water velocity.

Table 2 shows that values for gross daily production and community respiration were, on average, about 50 percent higher for the diurnal model compared to the slack. The diurnal model also estimated slightly higher maximum respiration and average dark respiration. The same holds for comparing estimates obtained by the multi-probe slack and diurnal methods (readings from all four probes were averaged before calculations of production rates). While metabolic rates were affected by water velocity, the P:R ratio does not appear to change. If P:R changes with an increase in water velocity, the change was not measurable in this study. The range of velocities encountered over the 16 day experiment may not have been large enough to demonstrate a change in P:R. The range of P:R for the diurnal methods (1.0 to 1.2) fell within the range of the slack methods (0.9 to 1.5). Increases in average velocity and therefore production would increase biomass or standing crop (Conover, 1968). Respiration also increased with water velocity but a P:R ratio greater than 1 would allow a net gain in biomass.

Results from the Eulerian method were comparable to the other methods but with reservation. All metabolic rate estimates (Table 2) fell close or within the range of estimates made by other methods. While the slack and diurnal methods showed a certain amount of variability (shown by standard error bars, Figures 12 & 13) one can still distinguish a line with respiration during the dark hours and production during daylight hours (a diel pattern of net production). The average net production line for the Euler method (Figure 14) did
not follow a typical diel pattern and showed maximum production in the early evening. The criteria used by the computational model (duration of stability required and maximum excursion of velocity over that time period) were manipulated to try to find better criteria. It was noted in successive trials that gross daily production could go as low as 3.1 gm O$_2$ m$^2$ day$^{-1}$ and as high as 7.8 gm O$_2$ m$^2$ day$^{-1}$ depending on the water velocity criteria. A diel pattern in net production was never encountered. Water velocity measurements and probe calibration could affect the outcome of the Eulerian model in regards to field technique.

The Eulerian method relies on accurate measures of water velocity to calculate residence time of water between the probes. Overestimation of velocity would reduce residence time estimates and increase estimated production rates. It was assumed for this study that 30 cm was an adequate level, within the canopy, for measuring water velocity. Gambi et al. (1990) show velocity profiles taken in a flume within a Z. marina community. A two layer flow is shown for free stream velocities as low as 5 cm sec$^{-1}$ with a high speed flow over the top of the canopy and flows under 1 cm sec$^{-1}$ within the canopy. If the current meter were close to the top of the canopy, or were to periodically peek over the canopy, water velocities would be overestimated. Since vertical profiles of water velocity were not taken, it is unknown if 30 cm was the proper height to use.

Another source of error in estimating Eulerian production rates would be apparent as a result of a two layer flow. If the DO concentration in the upper layer is not the same as the lower layer the assumption of a well mixed water column is lost. Temperature stratification can occur as show in Figure 11. Stratification would set up another diffusive boundary layer between the canopy flow and the free stream. As the parcel of water travels from probe to probe an unaccounted for flux of oxygen would lead to errors. And since the process is more than likely variable, more variability is introduced. Variability in mixing between the two layers across the bed could also refute the assumption that a DO
front travels across the seagrass bed. The DO front was assumed for flows that did not follow a line from upstream probe to downstream probe.

Probe calibration and drift could also have had a significant affect on production estimates. The dome, slack, and diurnal methods avoided this problem by using one probe. The probe would have had to drift significantly over a 5 or 10 minute sampling period to affect productivity measurements. Since two probes were used their intercalibration must be precise. If one probe drifted “up” (exaggerated higher than real DO concentrations) while another probe drifted “down”, then production rate calculations included drift error. If net production were zero, production measured one direction would have shown as respiration, while production measured when water flowed the opposite direction would have been overestimated. Water samples were taken from the field for calibration checks by comparison to Winkler titration’s. Lack of experience with the Winkler method diminished reproducibility and yielded inconclusive results.

The Lagrangian method would seem to have been subject to the same problems. It was not immune to probe calibration problems and two layer flow problems, but may have been less sensitive to velocity changes. There was no restriction on water velocity as a parcel of water flowed from one probe to another. Figure 15 shows 16 days pooled by hour into a “Lagrangian day”. There is a very noticeable difference between this figure and that of Figure 14 for the Eulerian method. The variability shown by standard error is visually less. The diel pattern shown by this method indicates that, with good probe calibration, it may be very effective for estimating metabolic parameters. Net production peaked around 1000 hrs (as occurred with the diurnal and slack methods). The evening respiration rates appear overestimated (compared to other methods in this paper) with a maximum respiration of about 2500 mg O$_2$ m$^2$ hr$^{-1}$.

Maximum production rate for the Lagrangian method (512 mg O$_2$ m$^2$ hr$^{-1}$) was low compared to other methods while the estimate of gross production was nominal. All
respiration parameters were larger than any other method. The DO concentration data and production data were reviewed for each probe with an interesting finding. Most of the calculations made by the Lagrangian model were made when the water mass was moving west to east. On average, for night and day, the eastern probe readings were lower than the western probe. It is conceivable that probe drift has lowered the Lagrangian production rate curve. Production rates and respiration rates were underestimated and overestimated, respectively, causing the entire curve to be lowered.

Figure 16 show the results obtained by the diurnal, Eulerian, and Lagrangian models in estimating NAP1 vs. water velocity. Where possible, none of the criteria about maximum or minimum water velocity, velocity changes over a time interval, nor the length of the time interval was changed. NAP1 rates were grouped into velocity ranges.

The diurnal method showed increasing gross production with water velocity until the 1.2 to 8.0 cm sec\(^{-1}\) range where it is depressed. Wheeler (1980) suggests that in high rate flows diminished productivity can be the result of a limiting nutrient. Wheeler states that increased water velocity will show no enhancement in production rates. Even though the high flow rate enhances transport across the boundary layer the limiting material must be there to be transported. But given the positive relationship between biomass and velocity regime (up to 51 cm sec\(^{-1}\)) shown by Conover (1968), a limiting nutrient seems unlikely. If a nutrient were limiting, gross production values should level off, not decrease. One of the assumptions made by the diurnal method is that the time histories of the two parcels of water measured at the beginning and end of the sampling period are to be similar. It may be possible that higher velocity flows cannot use this assumption.

The Eulerian method shows increasing net production with water velocity but the Lagrangian method shows the opposite. With problems of velocity measurement, reaeration, and probe calibration mentioned earlier, these values should be considered with
skepticism. Also, the values shown in Figure 16 are within the same numerical range of published data taken inside small chambers and domes. Rates over velocity ranges cannot be shown as statistically different.

CONCLUSIONS

It is interesting that the results obtained from the dome and slack methods are similar when other studies (Kemp & Boynton 1980, Odum 1956) would have one believe that the slack method should have estimated higher rates. This suggests that periods of slack water have an effect similar to placing a dome over the seagrass. Given the similarities, the slack method appears to be a good candidate for long term studies of seagrass beds if better estimates of reaeration can be made.

The relationship between production rates and water velocity has been shown with two open water methods (slack and diurnal) qualitatively and quantitatively. However further research is needed to confirm or disprove assumptions made about water flow over a seagrass bed. The dynamics of water flow may corrupt the assumption made about travel history of water parcels required for the diurnal method. Stratification and the possibility of two layer flows corrupt assumptions made about water velocity and vertical mixing made by all open water methods. Water flow dynamics may impede DO traveling as a front as was assumed for the Eulerian and Lagrangian methods. Assumptions were made regarding the flow of water; it is evident in this study that these assumptions are not always valid.

The scale of this study needs to be considered if repeated in a different current regime. At higher velocity flows upstream/downstream DO differences will become smaller. To compensate for this the probes must be separated by a greater distance. In an ideal setting the current would flow in only one direction, or have a strong bi-directional regime. Probes could be placed along a flow path allowing upstream/downstream
differences to be measured at different scales. This study was done on a scale that may not be able to show a strong relationship between water velocity and production.

The models ranged from the simple diurnal model, to the more complicated Lagrangian, to the more complex Eulerian. The complexity of each model is reflected in the number of lines of code required to implement each model. The diurnal model can use a single probe and is computationally simple. The Lagrangian model is complicated by the fact that two well calibrated probes are needed. Computationally it is a little more sophisticated since there are water column criteria that must be met. The Eulerian model is the most complex. Two well calibrated probes are needed and more assumptions are made about valid sampling points. The assumption of having a uniform flow for an interval of time to yield a valid sampling period is necessary to the method, but may not be possible in a highly variable seagrass bed. The numerical implementation of the assumptions were repeatedly varied to try to find the “magic combination”. None was found. Simplicity and good results are directly proportional to each other.

The Lagrangian method would be interesting to retry while paying better attention to probe calibration. Vertical profiles of water velocity compared with canopy height would be need to be studied to determine if there is an optimal depth to measure water velocity. It may also be wise to perform a sensitivity analysis on the model to see how sensitive it is to errors in water velocity measurement.

Further research is also needed to test the occurrence of DO gradients traveling as fronts. Further use of the diurnal method would require a test of the assumption regarding time histories of water parcels across the seagrass bed.

Future work could continue from this data set. It would be interesting to compare where in the 16 day period each model make calculations. Are there times when the models each make production estimations simultaneously? Are the production rates different? If
there are places where the methods overlap is there a difference in the physical environment compared to where the methods do not overlap? Could each method have an optimum environment that consistently appears during some phase of the neap to spring tidal cycle?

Another study that may be accomplished from the same data set would compare the P:R ratio as a function of timing in the neap-spring cycle. Do spring waters bring in nutrients that reinforce photosynthesis or do they bring in organic matter that enhance the respiration parameters?

In this study, different models were applied to the same data set collected from an established and stable seagrass community. Experimental design was able to minimize the effects of differing community structures due to seasonal and temporal variation. While seasonal and temporal variation were kept to a minimum, different methods showed variability in estimates of metabolic parameters. The metabolic parameter variability is a result of the day to day environmental variability encountered over the 16 day period. This study demonstrates that method choice plays a role in experimental outcome and must be considered in experimental objectives and design.
APPENDIX A

DO and Temperature

All DO and temperature measurements were taken with an Endeco/YSI Type 1125 (referred to here as T1125), 4 channel pulsed DO measurement system. Each probe has a pulsed polarographic (Clark type) oxygen sensor and thermister for temperature. In the field power was provided by a 12 VDC battery, the controller box was housed inside a plastic container to shield it from salt air, and probe housings (supplied by Endeco/YSI) were added to allow probes to be submerged. The T1125 controller box provides electronic control of the probes and digitizes probe readings that correspond to temperature and DO. The digitized numbers are sent from the controller box through an RS-232 computer interface. Typically a PC running the companion T1125 software receives the numbers, performs calculations based on calibration parameters, and displays and logs the measurements. Since it was not practical to deploy a PC laptop computer, a Tattletale 5F-LCD computer was programmed to receive the T1125 data, affix a time stamp, and store the DO and temperature data along with the water velocity data (discussed later). DO and temperature data collected by the Tattletale was moved to a Sun IPX UNIX workstation for processing. The computational sections of the T1125’s BASIC program (provided by Endeco/YSI) were translated into Matlab® (numerical computation and visualization software by The Mathworks, Inc.). Oxygen concentrations and temperature were then computed based on calibration coefficients obtained from the T1125’s calibration procedures (Endeco/YSI T1125 user manual). Calibration of the DO sensors was accomplished with Endeco’s extensive four-point calibration before and after deployment.

Water Velocity

Water column velocity was measured with a Marsh-McBirney model 721 electromagnetic current meter. Water velocity was recorded by measuring 2 channels of
voltages (magnitude of velocity in X and Y directions) made available from the current meter’s recorder output. Signal conditioning circuitry (design provided in Onset manuals) converted the bi-polar (positive and negative) voltages of the current meter into a uni-polar voltage required by the Tattletale analog-to-digital (A/D) converter. The digitized numbers from the A/D converter were stored with DO, temperature and a time stamp during data collection. Like the DO and temperature data, the digitized numbers were transferred to Matlab®. Calibration coefficients were then applied to the data to obtain water velocity measurements in cm sec⁻¹.

The current meter and computer circuit interface were flume calibrated before and after the experiment at velocities ranging from 0 to 14 cm sec⁻¹ (Velocities encountered during the experiment ranged for near zero to 7 cm sec⁻¹). For calibration, an 8 cm weighted tube was timed with a stop watch as it traveled 2 meters in the flume. Three replicates of travel time and a minimum of five readings from the data logger, taken as the weighted tube traveled, were averaged for each velocity. The water depth was ca. 10 cm and the center of the current probe was placed 6 cm from the bottom of the flume and centered in the 0.5 meter wide flume. Calibration was accomplished for all four directions (+X, -X, +Y, and -Y) measured by the probe before and after the experiment. Voltages proportional to velocity were digitized by the A/D interface. The integer numbers were regressed against the velocities recorded for the weighted tube to obtain calibration curves relating the digitized numbers to water velocity. Only slight changes were noted between calibrations but the post-experiment calibration was used since it had more calibration points at slower velocities for the regression calculations. The choice was based on low average velocities between 1 and 2 cm sec⁻¹ encountered during deployment.

Sampling in the flume, and later in the field, was at 10 Hz for 15 seconds and averaged. Logging of water velocity readings was simultaneous with DO data since the Tattletale computer logged water velocity and DO.
Logging DO, temperature and velocity

The T1125 controller box has its own internal timer and was set to take readings every 5 minutes. The Tattletale (TT) computer was programmed to synchronize itself to this timer and to take velocity measurements simultaneously.

The TT has an internal clock capable of tracking year, month, day, hour, minute, and seconds, and could therefore record a time stamp with data. One minute before data was anticipated from the T1125 the current meter was turned on to warm up (via relays controlled by the TT). The TT then started to watch for data from the T1125 ten seconds before it’s expected arrival time (this window more than allowed for slight timing differences between the T1125 and TT). Upon arrival of the T1125 data, a time stamp was stored in memory along with the T1125 data. Readings were then taken from the current meter, stored in memory, and the current meter was turned off. The TT went to sleep for 4 minutes and repeated the cycle again. The BASIC code (TxBasic by Onset) used in the TT follows (MMB refers to the Marsh-McBirney current meter):

```
// Routine to Monitor and store readings from the MMB and the
// Endeco T1125
// Initial Version 8 Apr 93 Bill Seufzer
// Mod 25 Apr 93 - 5 Min sample with Endeco
// - longer sampling for MMB
// - improve zero current for MMB
 cbreak alldone

// Set the internal clock
gosub SetTime

// Set up the Serial port for the Endeco
gosub alternateClock
gosub UARTnewbaud

// Initialize the MMB
pclr 2,3
XVel! = 0
YVel! = 0
XSlope! = -0.022
XInter! = 37.25
YSlope! = -0.022
YInter! = 38.72

// Wait for Pin 9 (KeyPad center) - press when out in field
```
dispaly "9"

WaitNine:
sleep 200
if pin(9) <> 0 goto WaitNine

// Initialize and wait for Endeco
SoftStart:
sleep 0
df=0
dfcpy=df
display "----"
print "Syncing to Endeco"
itext df,30500
iff dfcpy = df-42
  otext dfcpy
else
df = dfcpy
endif
display "6o"
print "synch'd"

// Start looping
TopLoop:
sleep 0
//sleep 4 minutes -15 secs for Current, then turn on MMB
print "Sleep 4 Min.....pin 10 for data"
for dd = 1 to 45
  sleep 500
  if pin(10) = 0 gosub DumpData
  if pin(9) = 0 goto SoftStart
next dd
print "MMB On"
pset 2,3
//should only have to wait 1 min for Endeco
print "Sleeping 45 sec"
sleep 4500
display "E??"
print "Awaiting Endeco"
itext df,6000
if dfcpy=df-42 dfcpy = df
time
print "Endeco Captured"
gosub GetCurrent
print "Current Displayed."
pclr 2,3
STORE df,#1,?(4),#1,?(3),#1,?(5),#1,?(2),#1,?(1),#1,?(0),#4,XCnt,#4,YCnt
goto TopLoop

// All Done
alldone:
display ""
pclr 2,3
gosub standardClock
gosub UARTdefault
stop

// Subroutine to Dump Data
DumpData:
dfcpy=df
def=0
PRINT
FOR B = 1 TO dfcpy/5
    otext df
    PRINT #2,GET(df,#1),"/",#2,GET(df,#1),"/",#2,GET(df,#1),":";
    PRINT #2,GET(df,#1),":",#2,GET(df,#1),":",#2,GET(df,#1),":";
    Xv=GET(df,#4)
    Yv=GET(df,#4)
    PRINT #10D,Xv,"",#10D,Yv
    sleep 25
NEXT B
print "End data......."
def=dfcpy
RETURN

// Subroutine to get the current speed
GetCurrent:
sleep 0
Samples = 30
XCnt = 0
YCnt = 0
FOR VelSample = 1 TO Samples
    XCnt=CHAN(5)/16 + XCnt
    YCnt=CHAN(6)/16 + YCnt
    sleep 50
NEXT VelSample
XCnt = XCnt/Samples
YCnt = YCnt/Samples
// divide by 16 from integer version. This was done because 12 bit D/A
// is left in upper bits. This did a shift right of 4 placing the 12
// bit number in the lower 12 bits of the 16 bit number
//print #10,XCnt," ",#10,YCnt
XVel!=(XSlope*XCnt)+XInter
YVel!=(YSlope*YCnt)+YInter
print #10.2F,XVel,#10.2F,YVel
disply #3.IF,sqr( YVel*YVel +  XVel*XVel)
return

// Subroutine to START 1 MINUTE BEFORE A 5 min period, WATCH FOR BUTTON 3
WaitPeriod:
disply ",",#3.1F,sqr(YVel*YVel + XVel*XVel)
RTIME
IF (?(1)+1)%5 = 0 GOTO EndWait
SLEEP 500
IF PIN(10) = 0 GOSUB DumpData
GOTO WaitPeriod
SLEEP 0
EndWait:
RETURN

// Subroutine to query user for date and time
SetTime:
RTIME
IF ?:5 = 93 Return
alternateClock:
asm $ 
TIME  equ H'43 ; address of LS byte of ? variable 
FRC   equ H'09 ; address of Free Running Counter 
OCR1  equ H'0B ; address of Output Compare Register 1 
ICR   equ H'0D ; address of Input Compare Register 
OCI   equ H'106 ; Output Compare Interrupt vector address 
TCSR1 equ H'08 ; address of Timer Control Status Register 1 
TCSR2 equ H'0F ; address of Timer Control Status Register 2 
TCSR3 equ H'1B ; address of Timer Control Status Register 3 
TCR   equ H'1C ; address of Time Constant Register (Timer2) 
TCRCOPY equ H'94 ; copy of the Timer2 Time Constant Register (TXBASIC) 
F_XTL equ D'24576 ; number Timer1 counts per 0.01 sec (fast crystal) 
S_XTL equ D'12288 ; number Timer1 counts per 0.01 sec (slow crystal) 
llda TIME ; get LS byte of current time (updated every .01 sec) 
wait1 slp ; wait for next interrupt 
cmpa TIME ; if interrupt was clock, this will have changed 
beq wait1 ; branch if not different (not a clock tick) 
ldd FRC ; get current Free Running Counter value 
addd #S_XTL ; add number of FRC ticks / 0.01 sec 
std OCR1 ; value of FRC for next clock tick 
; (handled automatically after first tick) 
aim #H'BC,TCSR3 ; disable Timer 2 interrupt 
llda #H'7E ; 'JMP' opcode 
sta OCI ; store at OCI vector 
ldd #H'FFC1 ; address of ALTCLK interrupt handler 
std OCI+1 ; address to 'JMP' to 
cira staa TCSR2 ; disable other Timer 1 interrupts and output lines 
llda #H'08 ; 'interrupt on Timer 1 compare' bit 
sta TCSR1 ; allow Timer 1 interrupts to act as clock 
end 
return 

standardClock:
asm $ 
llda TIME ; get LS byte of current time (updated every .01 sec) 
wait2 slp ; wait for next interrupt 
cmpa TIME ; if interrupt was clock, this will have changed 
beq wait2 ; branch if not different (not a clock tick)
ldaa #H'02
staa TCSR1 ; stop Timer 1 interrupts
ldaa TCRCPY ; get original value of Timer2's Time Constant Register
ldaa TCR ; and restore it
ldaa #H'52
staa TCSR3 ; enable Timer 2 interrupts to act as clock
end
return

// These subroutines can be used to get many different baud rates from the
// Tattletale's main UART but you should first set up the alternate system
// clock. See the document ALTCLOCK.DOC and sample program ALTCLOCK.TXB.

// The first subroutine causes Timer2 to be used as the baud rate generator
// for the UART and allows you to pick one of the standard baud rates. In
// this sample, we use the baud code assuming we have a fast crystal and
// want a baud rate of 300. You can choose the constant you want.
// The second subroutine returns the UART to its default condition.

// Subroutine #1 to allow any baud rate

UARTnewbaud:
asm $,
RMCR equ H'10 ; address of Rate/Mode Control Register (for UART)
TRCSR1 equ H'11 ; address of Tx/Rx Control Status Register 1 (for UART)

FB_38400 equ 1 ; baud code for fast crystal, 38400 baud
FB_19200 equ 3 ; baud code for fast crystal, 19200 baud
FB_9600 equ 7 ; baud code for fast crystal, 9600 baud
FB_4800 equ 15 ; baud code for fast crystal, 4800 baud
FB_2400 equ 31 ; baud code for fast crystal, 2400 baud
FB_1200 equ 63 ; baud code for fast crystal, 1200 baud
FB_600 equ 127 ; baud code for fast crystal, 600 baud
FB_300 equ 255 ; baud code for fast crystal, 300 baud

SB_38400 equ 0 ; baud code for slow crystal, 38400 baud
SB_19200 equ 1 ; baud code for slow crystal, 19200 baud
SB_9600 equ 3 ; baud code for slow crystal, 9600 baud
SB_4800 equ 7 ; baud code for slow crystal, 4800 baud
SB_2400 equ 15 ; baud code for slow crystal, 2400 baud
SB_1200 equ 31 ; baud code for slow crystal, 1200 baud
SB_600 equ 63 ; baud code for slow crystal, 600 baud
SB_300 equ 127 ; baud code for slow crystal, 300 baud

aim &HF5,TRCSR1 ; disable UART while changing its setup
oim &H20,RMCR ; select Timer2 as baud rate generator
aim &HBC,TCSR3 ; disable Timer2 from causing interrupt, use E clk
ldaa #SB_4800 ; load baud code for: SLOW crystal, 4800 baud
staa TCR ; store in Time Constant Register (Timer2)
oim &HA,TRCSR1 ; enable UART
end
return

// Subroutine #2 to reset UART back to its default state

UARTdefault:
asm $,
aim &HF5,TRCSR1 ; disable UART while changing setup
aim &HDF,RMCR ; baud rate from crystal
oim &H52,TCSR3 ; enable Timer2 interrupts and E/128 clock
ldaa TCRCpy ; get original value of Time Constant Register
staa TCR ; restore it
oim &HA,TRCSR1 ; restart UART
end
return
APPENDIX B

Matlab® Code for Dome Model

The following is a summary of how the dome model is computed. It is followed by the Matlab® routines that implement the model.

1) Readings of DO are in a column vector array. Each array index represents a 5 minute sampling interval. The first array position represents \( t = 0 \), the first sampling period.

2) An array index is used as a counter through time, starting with \( t = 5 \).

3) At each index production rate is calculated as above. \( \Delta t = 5 \) minutes, \( \text{Vol} = 260 \) liters, \( \text{Area} = 0.78 \) m\(^2\).

4) The result is a column vector of production rates.

5) Production rates are grouped by hour.

6) Production rates within each hour are averaged and standard deviations are calculated.

7) Production rates for each hour interval are sent to a routine that implements rules for estimating, gross production, community respiration, etc., as defined in Odum & Hoskin (1958).

The following Matlab® code performs the dome model summarized above. The purpose for other functions are documented on the line previous to the function call and are not listed here.
% function [D] = Dome(x)

global Abscissa Licor Oxmgl Tc

% a full 24 hr period
db=78; % 78 => 16:10 on julian day 158
de=366; % 366 => 16:10 on julian day 159

% Calculate production parameters for Dome 1, splined data, 24 hr period
% 2 Sep 94
if x == 6
    t=1; % 1 hr interval to avg over
    % select 24 hours of data
    A(:,1)=Abscissa(db+1:de,7);
    A(:,2)=DomePT(Oxmgl(db:de,5),5);
    % determine the photoperiod
    pp=PhoPer(Abscissa(db:de,7),Licor(db:de,4));
    % make sure all rows have data
    AA=NoRowsNaN(A);
    % average grouped by 1 hour
    AG=AvdGroup(AA(:,1),AA(:,2),t);
    % Calculate metabolic parameters, and plot
    SP=SpProd(AG(:,1),AG(:,2),pp);
    PlotNP(AG(:,1),[AG(:,2) AG(:,3)],[-2500 500 2500],pp(1) pp(2),'Dome 1');
    set(gca,'nextplot','add');
    plot(SP(:,1),SP(:,2),'r.');
    % save results
    d=DProd(SP);
    d(7)=sum(AG(:,6));
    r=MetRes(1,d);
    wklwrite('output/WK1/PvTdl1','AG');
    print -deps output/Dome1NP.eps
end

function [P] = DomePT( d, t)
% DomePT(d,t) Takes a vector of DO readings (d), and the time difference (t), and returns a 1 col array of Production values as a function of time.
% d=[mg/L], t=[min], P=[mgO2/m2/hr]
% Dome volume is 260L, Area is 0.7854 m2

rows=size(d,1);
for x=1:rows-1
    DJdif(x)=d(x+1)-d(x);
end
DJdif=DJdif';
P(:,1)=((60/t)*260/0.7854).*DJdif;
return
APPENDIX C

Matlab® Code for Slack Model

The following is a summary of how the slack model is computed. It is followed by the Matlab® routines that implement the model.

1) Readings of DO, Depth, and Water velocity are in arrays as in the previous dome model.
2) An array index is used as a counter through time (starting with t=5).
3) Water velocity values from the previous, present, and next readings are averaged.
4) The maximum and minimum water velocities are computed.
5) If the average current for the interval is less than 0.5 cm sec\(^{-1}\), and the minimum and maximum current do not differ by more than 0.1 cm sec\(^{-1}\), the routine continues to calculate production rates, otherwise time is incremented and a jump is made back to step 3.
6) Production rate is calculated as above. Depth is the average depth over the interval.
7) The result is a column vector of production rates.
8) Production rates are grouped by hour.
9) Production rates within each hour are averaged and standard deviations are calculated.
10) Production rates for each hour interval are sent to a routine that implements rules for estimating gross production, community respiration, etc., as defined in Odum & Hoskin (1958).

The following Matlab® code performs the slack water model summarized above. The first listing is part of a larger function that organizes the needed data, generates a plot, and saves the results. A similar function calls function SlackATLP to perform the model with the probe measurements averaged. The second function actually performs the slack model.
% 5 - Production vs Time of day, individual probes
% if x == 5
  t=1;
  for probe=1:4
    A=SlackATLP(probe,0.5,0.1);
    % eliminate rows without data
    AA=NoRowsNaN(A);
    % average each hourly group
    AG=AvgGroup(AA(:,2),AA(:,5),t);
    % set the photo period
    pp=[5 19];
    % calculate metabolic parameters and plot.
    SP=SpProd(AG(:,1),AG(:,2),pp);
    st=('Slack Probe ' num2str(probe));
    PlotNP(AG(:,1),[AG(:,2) AG(:,3)],[ -2500 500 2500], [pp(1) pp(2)],st);
    set(gca,'nextplot','add');
    plot(SP(:,1),SP(:,2),'r.');
    % save the results
    d=DProd(SP);
    d(7)=sum(AG(:,6));
    r=MetRes(probe+2,d);
    base=['PvTslk1 ' num2str(probe)];
    eval(['print -deps output/' base '.eps'])
  end
end
function [ATLP] = SlackATLP(probe, max, dif)

% function [A,T,L,P] = SlackATLP(probe, max, dif) calculates production for
% any probe, at water velocities < max, where the difference in velocity is
% < dif. ATLP is an array which contains the point in time the event
% occurred - Abscissa(:,[6 7]), the temperature - T, light level -L, and the
% net production. T=[deg C], L=[uE/s], P=[mgO2/m2/hr].

global Abscissa Cur Depth Licor Oxmg Tc

DO=Oxmg(:,probe);
Vel=Cur(:,6);
I=Licor(:,3);
T=5;

rows=size(Vel,1);
i=1;

for n=2:rows-1
    if Vel(n) <= max
        if abs(Vel(n+1)-Vel(n-1)) <= dif
            DODif=DO(n+1)-DO(n-1);
            Iavg=(1e6/(T*60))*(I(n)+I(n+1));
            Prod=(60/(T^2))*Depth(n)*DODif*1000;
            ATLP(i,1)=Abscissa(n,6);
            ATLP(i,2)=Abscissa(n,7);
            ATLP(i,3)=Tc(n,probe+1);
            ATLP(i,4)=Iavg;
            ATLP(i,5)=Prod;
            i=i+1;
        end
    end
end
MATLAB® Code for Diurnal Model

The following is a summary of how the diurnal model is computed. It is followed by the MATLAB® routines that implement the model.

The MATLAB routine that makes these calculations is summarized as follows:
1) Readings of DO, Depth, and Water velocity are in arrays as in the previous models.
2) An array index is used as a counter through time (starting with t=5).
3) Water velocity values from the previous, present, and next readings are averaged.
4) The maximum and minimum water velocities are computed.
5) If the average current for the interval is greater than 0.5 cm sec\(^{-1}\), and the minimum and maximum water velocities do not differ by more than 0.15 cm sec\(^{-1}\), the routine continues to calculate production rates, otherwise time is incremented and a jump is made back to step 3.
6) Production rate is calculated as above. Depth is the average depth over the interval. Reaeration uses averages of depth, current velocity, DO, and the saturation level of DO over the interval.
7) The result is P, a column vector of production rates.
8) Production rates are grouped by hour.
9) Production rates within each hour are averaged and standard deviations are calculated.
10) Production rates for each hour interval are sent to a routine that implements rules for estimating net production, gross production, etc., as defined in Odum & Hoskin (1958).

The following MATLAB® code performs the diurnal model summarized above. The first listing is part of a larger function that organizes the needed data, generates a plot, and saves the results. A similar function calls DiurnalATLP to perform the model with the probe measurements averaged. The second function actually performs the diurnal model.
if x == 6
  t=1;
  for probe=1:4
    A=DiurnalATLP(probe,10,0.15);
    AA=NoRowsNaN(A);
    AG=AvgGroup(AA(:,2),AA(:,5),t);
    pp=[5 19];
    SP=SpProd(AG(:,1),AG(:,2),pp);
    st=['Diurnal Probe ' num2str(probe)];
    PlotNP(AG(:,1),[AG(:,2) AG(:,3)],[2500 500 2500],[pp(1) pp(2)],st);
    set(gca,'nextplot','add');
    plot(SP(:,1),SP(:,2),'r.');
    d=DProd(SP);
    d(7)=sum(AG(:,6));
    r=MetRes(probe+7,d');
    base=['PvTdiur ' num2str(probe)];
    eval(['print -deps output/' base '.eps']);
  end
end
function [ATLP] = DiurnalATLP(probe,per,dif)

%function [ATLP] = DiurnalATLP(probe,per,dif) calculates production for
% any probe, over period per, where the max difference in velocity is
% < dif. ATLP is an array which contains the point in time the event
% occurred - Abscissa(:,[6 7]), the temperature - T, light level -L, and
% net production. T=[deg C], L=[uE/s], P=[mgO2/m2/hr].

global Abscissa Cur Depth Licor Oxmg Tc CSat

DO=Oxmg(:,probe); 
Vel=Cur(:,6); 
I=Licor(:,3); 
T=5;

rows=size(Vel,1); 
i=1;

for n=2:rows-1
    if Vel(n) >= 0.5
        vels=[Vel(n+1);Vel(n);Vel(n-1)];
        vels=NoRowsNaN(vels);
        cmax=max(vels);
        cmin=min(vels);
        deps=[Depth(n+1);Depth(n);Depth(n+1)];
        depavg=mean(deps);
        dos=[DO(n+1);DO(n);DO(n-1)];
        csats=[CSat(n+1);CSat(n);CSat(n-1)];
        if abs(cmax-cmin) <= dif
            DODif=DO(n+1)-DO(n-1);
            Iavg=(1e6/(T*60))*(I(n)+I(n+1));
            k=EOk(mean(vels),depavg);
            R=Flux(k,mean(dos),mean(csats));
            Prod=((60/(T*2))*depavg*DODif*1000)-(R*depavg*1000);
            ATLP(i,1)=Abscissa(n,6);
            ATLP(i,2)=Abscissa(n,7);
            ATLP(i,3)=Tc(n,probe+1);
            ATLP(i,4)=Iavg;
            ATLP(i,5)=Prod;
            i=i+1;
        end
    end
end
APPENDIX E

Matlab® Code for Eulerian Model

The following is a summary of how the Eulerian model is computed. It is followed by the Matlab® routines that implement the model.

1) All necessary data are in arrays as in the previous models.
2) An array index is used as a counter through time (starting with t=0).
3) The index of time + 20 minutes is determined. Present time to this index is considered “the interval”.
4) Averages are computed for water velocity (speed and direction), depth, and the saturation level of DO.
5) The maximum and minimum water velocities are computed.
6) If the average water velocity for the interval is greater than 0.5 cm sec\(^{-1}\), and the minimum and maximum velocities do not differ by more than 0.4 cm sec\(^{-1}\), the routine continues to calculate production rates, otherwise time is incremented and a jump is made back to step 3.
6) Current direction is used to determine the upstream and downstream probes.
7) Distance is calculated based on direction. Residence time, \(\Delta t\), is calculated from distance and average velocity.
8) Production rate is calculated as above. Depth is the average depth over the interval. Reaeration uses averages of depth, velocity, DO, and the saturation level of DO over the interval.
9) The result is a column vector of production rates.
10) Production rates are grouped by hour.
11) Production rates within each hour are averaged and standard deviations are calculated.
12) Production rates for each hour interval are sent to a routine that implements rules for estimating gross production, community respiration, etc., as defined in Odum & Hoskin (1958).
The following Matlab® code performs the Eulerian model summarized above. The first listing is part of a larger function that organizes the needed data, generates a plot, and saves the results. The second function actually performs the Eulerian model.

```matlab
if x == 1
    E=EulerAPIVD(0.4,0.5,10,20); %E=[Abs6 Abs7 Prod I Vel Dir Dif]
    % Eliminate empty rows
    E=NoRowsNaN(E);
    Pc=E(:,3)-E(:,7);
    % Average by the hour
    AG=AvgGroup(E(:,2),Pc,1);
    % set the photo period
    pp=[5 19];
    % calculate metabolic parameters and plot
    SP=SpProd(AG(:,1),AG(:,2),pp);
    st=('Eulerian');
    PlotNP(AG(:,1),[AG(:,2) AG(:,3)],[-2500 500 2500],[pp(1) pp(2)],st);
    set(gca,'nextplot','add');
    plot(SP(:,1),SP(:,2),'r.');
    % save the results
    d=DProd(SP);
    d(7)=sum(AG(:,6));
    r=MetRes(13,d);
    print -deps output/PvTEul.eps
end
```
function [Eu] = EulerAPIVD(Thresh,VMin,VMax,Dur)

% function [E] = EularAPIVD(Thresh,VMin,VMax,Dur) is based on
% an Eulerian algorithm where Thresh is the threshold of variation in
% velocity over the time period Dur; VMin to VMax is the range of velocities
% allowed for the period. The vector returned is:
% Abscissa(:,[6 7]) as a time stamp, P - production rate [mgO2/m2/hr],
% I - average light intensity over the period uE/m2/s,
% V - avg velocity over the period Dur in cm/sec,
% D - direction of flow in radians. d - diffusion rate mgO2/m2/hr
% Thresh=[cm/sec], Dur=[min] multiple of 10 min.
% updated from EularPI.m on 7 Mar. Added globals and allowed Thresh
% and Dur parameters.

global Abscissa Cur Depth Licor Oxmg Tc Wind CSat

Vel=Cur(:,[6 7]);
DO=Oxmg;
I=Licor(:,3);
D=50;
T=5;
rows=size(Vel,1);

%Arguments
Mag = 1;
Dir = 2;
N = 1;
S = 3;
E = 2;
W = 4;
True=l;
False=0;
n=1;
nnumel=Dur/5;
for i=1:rows-nnumel
    j=i+nnumel;
    %calc avg direction
    xavg=mean(Cur(i:j,4));
    yavg=mean(Cur(i:j,5));
    dir=atan2(yavg,xavg);
    dirdeg=dir*180/pi;

    %calc velocities
    vels=Vel(i:j,Mag);
    vmin=min(vels);
    vmax=max(vels);
    vavg=mean(vels);

    % determing average depth and saturation DO level
    davg=mean(Depth(i:j));
    CSatavg=mean(CSat(i:j));

    if (abs(vmax-vmin) <= Thresh) & (vavg > VMin) & (vavg < VMax)
        Inten=(1e6/(T*60))*sum(I(i+1):I(j));
    end
end
%Based on dir calculate DOdif and distance travelled
if dir <= pi/4 & dir >= (-pi/4)
    DOdif=DO(j,E)-DO(j,W);
    Dist=abs(D*cos(dir));
elseif dir <= (3*pi/4) & dir >= pi/4
    DOdif=DO(j,N)-DO(j,S);
    Dist=abs(D*sin(dir));
elseif dir <= pi/4 & dir >= (-3*pi/4)
    DOdif=DO(j,S)-DO(j,N);
    Dist=abs(D*sin(dir));
else
    DOdif=DO(j,W)-DO(j,E);
    Dist=abs(D*cos(dir));
end
DelT=(Dist/vavg)/36; %=[hour] 100cm/m, 3600 s/hr
Prod=(((DOdif*1000)*davg)/DelT;
%compute diffusion
%Kf=TFk(vavg,Depth(i),wavg);
Kf=EOk(vavg,davg);
Df=Kf*(CSatavg-mean(DO(j,[1 2 3 4])));
Dif=Df*1000*davg;
Eu(n,:)=[Abscissa(i,6) Abscissa(i,7) Prod Inten vavg dir Dif];
    n=n+1;
end
end
APPENDIX F

Matlab® Code for Lagrangian Model

The following is a summary of how the Lagrangian model is computed. It is followed by the Matlab® routines that implement the model.

1) All necessary data are in arrays as in the previous models.
2) An array index is used as a counter through time (starting with t=0).
3) The index of time + 150 minutes is determined.
4) Total travel distance is calculated based on initial direction of travel.
5) DO readings are taken for all probes. One of these will later become the upstream probe.
6) Current magnitude is numerically integrated into travel distance until more than 150 minutes have passed or until distance calculated in 4 is reached.
7) If 150 minute travel time was not exceeded, calculation continues, otherwise time is incremented and a jump is made to step 3.
8) Current direction is used to determine the upstream and downstream probes.
9) Averages are computed for velocity, depth, and saturation level of DO.
10) Production rate is calculated as above. Depth is the average depth over the interval. Reaeration uses averages of depth, velocity, DO, and the saturation level of DO over the interval.
11) The result is a column vector of production rates.
12) Production rates are grouped by hour.
13) Production rates within each hour are averaged and standard deviations are calculated.
14) Production rates for each hour interval are sent to a routine that implements rules for estimating gross production, community respiration, etc., as defined in Odum & Hoskin (1958).

The following Matlab® code performs the Lagrangian model summarized above. The first listing is part of a larger function that organizes the needed data, generates a plot, and saves the results. The second function actually performs the Lagrangian model.
function \( [L] = \text{Lagran}(x) \)

% function \( [L] = \text{Lagran}(x) \)
% this function documents the analysis performed on the GWArray data for
% the Lagrangian flow model.
%

global Abscissa Cur Depth Licor Oxmg Tc
if nargin==1
    r=0;
end
%
1 - Langrangian all Velocities
if x == 1
    \( L = \text{LagranAPIVD}(0,15) \); \( L = [\text{Abs6 Abs7 Prod I Vel Dir Dif}] \)
    % eliminate empty rows
    \( L = \text{NoRowsNaN}(L) \);
    \( P_c = L(:,3) - L(:,7) \);
    % average by the hour
    \( A_G = \text{AvgGroup}(L(:,2),P_c,1) \);
    \( A_G = \text{NoRowsNaN}(A_G) \);
    % establish the photoperiod
    \( p_p = [5 19] \);
    % calculate metabolic parameters and plot
    \( S_P = \text{SpProd}(A_G(:,1),A_G(:,2),p_p) \);
    \( t_s = ['\text{Lagrangian}'] \);
    \( \text{PlotNP}(A_G(:,1),[A_G(:,2) A_G(:,3)],[4000 500 1500],[p_p(1) p_p(2)],t_s) \);
    set(gca,'nextplot','add')
    plot(S_P(:,1),S_P(:,2),'r.' )
    % save results
    \( d = \text{DProd}(S_P) \);
    \( d(7) = \text{sum}(A_G(:,6)) \);
    \( r = \text{MetRes}(14,d') \);
print -deps output/PvTLag.eeps
end
function [L] = LagranAPIVD(Vmin,Vmax)

% function [L] = LagranAPIVD calcs a production table with the Abscissa
% Production rate, Light, Velocity, Direction and Diffusion rate.
% L is [Abscissa(i,6) Abscissa(i,7) Production[mg02/m2/hr] I[uE/m2/s]...
% Vel[cm/s] Dir[degrees] Dif[mg02/m2/hr].

global Abscissa Cur Depth Licor Oxmg Tc CSat

DO=Oxmg;
I  =  Licor(:,:3)  ;
Vel=Cur(:,[6 7]);
T=5;  %sampled at 5 min
PSep = 50;  % probe separation meters
MaxDev = 30;  %max allowable change in current direction (degrees)

%Arguments
Mag = 1;
Dir = 2;
N = 1;
S = 3;
E = 2;
W = 4;
True =1;
False = 0;
rows=size(Vel,1);
pt = 0;

for x = 2:rows-1
    BeginTime = x;
    EndTime = x+30;  %
    Time=x;

    %Get Current Mag & Dir
    U=[Vel(Time,1) Vel(Time,2)*180/pi];  %dir in degrees
    InitAng = U(Dir);

    %Calc Travel Distance
    Dist = [PSep*sin(U(Dir)) PSep*cos(U(Dir))];
    TotDist = max(abs(Dist(1)),abs(Dist(2)));
    %TotDist = PSep;

    %Get Initial DO
    %InitDO = DO(x,:);
    InitDO=mean(DO([x-1 x x+1],:));

    Position = 0;
    Light = 0;
    NotThereYet = True;
    Broke = False;

    %Average these later
    SumVel = U(Mag);  %used to find the average velocity
    SumDep = Depth(x);
    SumCs = CSat(x);
    SumC = InitDO;
    Counts = 1;

92
while NotThereYet
    Position = Position + (U(Mag) * T^0.6); %60 sec/min / 100 cm/min
    Light = Light + I(Time);
    if abs(U(Dir) - InitAng) > MaxDev
        Broke = True;
        break
    end
    if Position >= TotDist
        NotThereYet = False;
    else
        Time = Time + 1;
        U = [Vel(Time, 1) Vel(Time, 2) * 180 / pi]; %dir in degrees
        SumVel = SumVel + U(Mag);
        SumDep = SumDep + Depth(Time);
        SumCs = SumCs + CSat(Time);
        SumC = SumC + DO(Time,:);
        Counts = Counts + 1;
    end
    if ((Time > rows - 1) | (Time > EndTime))
        Broke = True;
        break
    end
end

%If did not break this may be a valid point
if Broke == False
    AveTime = fix((BeginTime + Time) / 2);
    AveVel = SumVel / Counts;
    if (AveVel > Vmin) & (AveVel < Vmax)
        AveDep = SumDep / Counts;
        AveCs = SumCs / Counts;
        AveC = mean(SumC / Counts);
        Intensity = Light * (le6 / (Counts * T^60)); %uE/m2/s
        FinalDO = DO(Time,:);
        FinalDO = mean(DO([Time - 1 Time Time + 1],:));
        DirDeg = U(Dir);
        %disp(DirDeg);
        if (DirDeg <= 45 & DirDeg >= -45)
            DO1 = InitDO(W);
            DO2 = FinalDO(E);
            DirF = 1;
        elseif (DirDeg > 45 & DirDeg <= 135)
            DO1 = InitDO(S);
            DO2 = FinalDO(N);
            DirF = 2;
        elseif (DirDeg < -45 & DirDeg >= -135)
            DO1 = InitDO(N);
            DO2 = FinalDO(S);
            DirF = 3;
        else
            DO1 = InitDO(E);
            DO2 = FinalDO(W);
            DirF = 4;
        end
end
if (DirF == 1 | DirF == 4)
    PR = ((DO2-DO1)*1000*AvgDep)/((TotDist/AvgVel)/36);
    %mgO2/m2/hr
    % 100cm/m 3600 s/hr
    Kf=EOk(AvgVel,AvgDep);
    Df=Kf*(AvgCs-AvgC);
    Dif=Df*1000*AvgDep;
    pt = pt + 1;
    L(pt,1)=Abscissa(AvTime,6);
    L(pt,2)=Abscissa(AvTime,7);
    L(pt,3)=PR;
    L(pt,4)=Intensity;
    L(pt,5)=AvgVel;
    L(pt,6)=DirDeg;
    L(pt,7)=Dif;
end %Vel range check
end % if Broke
end % for x
APPENDIX G

Matlab® Code for Metabolic Parameter estimation

The following is a summary of how metabolic parameters are computed. It is followed by the Matlab® routine that implements these calculations.

1) The maximum production rate is computed as the largest number in the production rate vector.
2) The maximum respiration rate is the smallest number in the production rate vector.
3) Mean dark respiration is the average value of all negative production rates not within the photoperiod.
4) NAP1 is the numerical integration of positive production rates during the photoperiod.
5) NAP2 is computed from the numerical mean of production rates between 1000 hours and 1400 hours integrated over 80% of the photoperiod.
6) Gross production is the numerical integration of production within the photoperiod plus the mean dark respiration over the photoperiod.
7) Community respiration is the mean dark respiration numerically integrated over 24 hours.
8) Production:Respiration is gross production divided by community respiration.
function [PR] = DProd(SP)

% function [PR] = DProd(SP,pho)
% takes an abscissa vector (SP(:,1)) (hour of the day), a net production
% rate vector (SP(:,2)=[mgO2/m2/hr]), SP(:,3) contains 1's for photoperiod.
% It returns a vector of metabolic parameter calculations (PR).
% IT IS ASSUMED THAT THE DATA SPANS A 24 HR PERIOD.
% Based on Odum & Hoskin (1958).
% %
% % PR(x) is defined as:
% % x = value, units
% % 1  = max Pr, mgO2/m2/hr
% % 2  = max Resp, mgO2/m2/hr
% % 3  = Average dark resp rate, gO2/m2/hr
% % 4 = NAP gO2/m2/day
% % 5 = NAP 1000-1400 gO2/m2/day
% % 6 = Gross prod, gO2/m2/day
% % 7 = Community Respiration, gO2/m2/day
% % 8 = Community P:R, Gross P/Comm Resp

PR=zeros(8,1);
delta=SP(2,1)-SP(1,1);  %delta t for integration

% maximum Production rate
PR(1)=max(SP(:,2));

% maximum Respiration rate
PR(2)=abs(min(SP(:,2)));

% average dark respiration rate
rpos=find(SP(:,2)<=0 & SP(:,3)==0);
PR(3)=abs(mean(SP(rpos,2)));

% Net Apparent Production over photoperiod
nap=find(SP(:,2)>0 & SP(:,3)==1);
PR(4)=sum(SP(nap,2)*delta)/1000;

% Net Apparent Production from mean of rates 1000 to 1400 hrs
% mean rate is assumed for 80% of photoperiod (Murray & Wetzel 1987)
phoVec=find(SP(:,3)==1);
last=size(phoVec,1);
phoPer=0.8*(SP(phoVec(last),1)-SP(phoVec(1),1));
ratesVec=find(SP(:,1)>=10 & SP(:,1)<=14);
AvgRate=mean(SP(ratesVec,2));
PR(5)=AvgRate*phoPer/1000;

% Gross prod =
GP=SP(:,2)+PR(3);
gpos=find(GP(:,1)>0 & SP(:,3)==1);
tot=sum(GP(gpos,1)*delta);
PR(6)=tot/1000;

% Community Respiration
PR(7)=PR(3)*24/1000;
% Community P:R
PR(8)=PR(6)/PR(7);
return
LITERATURE CITED


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