
Denis William Frazel
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ASPECTS OF PHYTOPLANKTON
CHLOROPHYLL a CARBON-SPECIFIC GROWTH RATES,
AND THE DISTRIBUTIONS OF CHLOROPHYLL a
AND PRIMARY PRODUCTIVITY
IN RELATION TO WATER COLUMN STRUCTURE
IN THE EASTERN NORTH ATLANTIC OCEAN

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
OCEANOGRAPHY

BY
DENIS WILLIAM FRAZEL

NOVA UNIVERSITY
1990
DOCTORAL DISSERTATION
OF
DENIS WILLIAM FRAZEL

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William A. Venezia

NOVA UNIVERSITY
1990
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I thank my parents for instilling in me the belief that I can accomplish anything I set my mind to, and I thank my wife, Rowena, for graciously contending with the trials and tribulations of a cranky graduate student.

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PREFACE

This dissertation consists of three chapters, two of which are presented in manuscript form. Chapter One is an introduction and review of the measurement of phytoplankton chlorophyll a carbon-specific growth rates. Chapter Two consists of the manuscript ASPECTS OF CHLOROPHYLL A CARBON-SPECIFIC GROWTH RATE IN THE EASTERN NORTH ATLANTIC OCEAN. It has been formatted in accordance with the specifications of the oceanographic journal Marine Ecology Progress Series. In Chapter Two, an evaluation of the short-term kinetics of the labeling time of natural phytoplankton populations in different oceanic regions showed that chl a labeling varied in relation to both environmental conditions and latitude. At subtropical stations rapid short-term increases in the activity of chl a were coincident with large (> 38%) increases in total photosynthetically available radiation. The rapid short-term increases resulted in overestimates of the growth rate. Overall though, a strong correlation between chl a carbon-specific growth rates and independently-derived assimilation numbers was evident. This strong correlation, particularly with end-of-day samples suggests that the chl a labeling technique for phytoplankton carbon-specific growth rate determination is applicable in different oceanic regions under broadly varying environmental conditions.

Chapter Three consists of the manuscript DISTRIBUTIONS OF CHLOROPHYLL AND PRIMARY PRODUCTIVITY IN RELATION TO WATER COLUMN STRUCTURE IN THE EASTERN NORTH ATLANTIC OCEAN. Chap-
Chapter Three has been formatted in accordance with specifications of the Journal of Global Biogeochemical Cycles. Chapter Three has been submitted under the co-authorship of G. Berberian for review by the Journal of Biogeochemical Cycles. In Chapter Three latitudinal variations in the megascale ($10^3$ km) distribution of biological properties were observed in relation to the water column structure between $60^\circ$N and $7^\circ$N in the Eastern Atlantic Ocean. High chl a concentrations in the northern latitudes were associated with a shoaling of the pycnocline. A secondary region of high chl a at $7^\circ$N was associated with a lens of low salinity Amazon River water. Productivity maxima were located south of Iceland, in the vicinity of the Azores Front, and at the Amazon River water feature.

The research described in Chapters Two and Three was performed during the Eastern North Atlantic section of the 1988 National Oceanic and Atmospheric Administration (NOAA) Global Change Expedition. Two appendices are included in the dissertation which contain pertinent Global Change Expedition data used in the manuscripts. Appendix One contains data relevant to Chapter Two, while Appendix Two contains data relevant to Chapter Three. A NOAA Data Report (Frazel, Berberian and Hitchcock 1989) containing complete data for the Global Change Cruise is also available. Reference lists are included at the end of Chapters Two and Three, while a master reference list is given at the end of the dissertation.
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Chapter I

Introduction
Phytoplankton growth rate can be defined in simple terms as the change in biomass per unit time. Growth rate \( (\mu, \text{d}^{-1}) \) is generally calculated by the equation:

\[
\mu = \frac{1}{C_p} \times \frac{dC_p}{dt}
\]

where \( dC_p/dt \) is the photosynthetic rate and \( C_p \) is the concentration of phytoplankton carbon, i.e. biomass (after Redalje and Laws 1981). In this scheme, measurements of photosynthetic rate and biomass are the factors that define the estimation of growth rate. Photosynthetic rate is primarily measured by the \(^{14}\text{C}-\text{CO}_2\) uptake method, developed by Steemann Nielsen (1952). Though widely used, reviews of the method by Eppley (1980) and Peterson (1980) suggest that uncertainties with the method may affect not only the accuracy of the observed rate, but the accuracy of subsequent growth determinations as well.

Of similar concern with respect to growth rate estimates is the accurate measurement of phytoplankton biomass. In the laboratory, cells may be counted directly, and converted to biomass estimates in terms of cell volume, carbon content, or cell surface area (Fogg, 1966). This is a straightforward task in the laboratory, but conducting these measurements at sea is an extremely labor-intensive project. Additionally, one is faced with the problems of isolating the phytoplankton fraction from the total plankton community, and differentiating between living and dead cells.
(Sakshaug, 1980). Other types of biomass estimates, as difficult as those described above, are detailed by Redalje and Laws (1981). The conclusion of these reviews is that in order to improve the estimate of phytoplankton growth rate more reliable means of measuring both biomass and photosynthetic rate must be developed.

A method for estimating phytoplankton growth rates and carbon biomass, proposed recently by Redalje and Laws (1981), addresses the problem of measuring living biomass. The procedure relies upon the labeling of chlorophyll a by $^{14}$C and the subsequent chromatographic isolation of chlorophyll a. The specific activity of the chlorophyll a fraction is determined, and converted into a chlorophyll a-carbon specific activity value designated $R^*$ (dpm $\mu$gC$^{-1}$) by Redalje and Laws (1981), by the equation:

$$R^* = \frac{\text{Chl a activity}}{\text{Chl a carbon} \times 0.7386} \tag{2}$$

where the Chl a activity is given in units of (dpm), Chl a carbon in units of ($\mu$g), and 0.7386 is the fraction of the molecular weight of chlorophyll a contributed by carbon. The total filtered particulate matter, designated $A^*$ by Redalje and Laws (1981) is divided by the chlorophyll a-carbon value to generate an estimate of phytoplankton carbon biomass:
where \( C_p \) is carbon biomass (\( \mu g \ L^{-1} \)), and \( A^* \) is the activity of the total filtered particulate matter (dpm \( L^{-1} \)).

Assuming exponential growth, an estimate of the chlorophyll a-carbon specific growth rate can be calculated by incorporating a photosynthetic rate measurement with the estimate of phytoplankton carbon biomass (Eq. 3) in the equation:

\[
\mu = \frac{1-Pt}{C_p T} \]

where \( P \) is the photosynthetic rate (\( \mu C \ L^{-1} h^{-1} \)), \( t \) is the time of incubation (h), and \( T \) is the incubation period as a fraction of one day (d) (Eq. 5, Redalje and Laws 1981).

Welschmeyer and Lorenzen (1984) suggested that since the chlorophyll a labeling technique proposed by Redalje and Laws includes the measurement of total carbon fixation (\( A^* \), Eq. 3), as well as photosynthesis (\( P \)), uncertainties with the \( ^{14}C \) technique (Eppley 1980) could be reflected in the growth rates. They proposed that the specific growth rate could be measured without an estimate of total carbon fixation.

Referring back to Equation 4, Welschmeyer and Lorenzen (1984) noted that:
where the value 1.05 accounts for isotope discrimination, and \( I^* \) (dpm ugC l\(^{-1}\)) is the specific activity of the dissolved inorganic carbon (DIC) supply.

By substituting Equations 3 and 5 into Equation 4, Welschmeyer and Lorenzen (1984) derived,

\[
\mu = \frac{\ln [1 - \frac{(1.05R^*)}{I^*}]}{t},
\]

this demonstrates that the activity of the total filtered particulate matter could, in fact, be eliminated from the specific growth calculation.

The Redalje and Laws (1981) chlorophyll a labeling technique and the Welschmeyer and Lorenzen (1984) modification rely on the assumption that the specific activity of chlorophyll a carbon and total phytoplankton cellular carbon are equivalent after a period of incubation.

This assumption raises three key questions: first, do the specific activities of chlorophyll a carbon and total phytoplankton cellular carbon attain an equilibrium; second, what is the time course over which this isotopic equilibration occurs; and third, is the method applicable to the open
The transition toward equilibrium can be defined by, or described with a conceptual model of a phytoplankton cell consisting of two compartments. The first compartment consists of chlorophyll carbon within the chloroplast. The chloroplast is contained within the second compartment, which consists of the total cellular carbon. The model cell is suspended in seawater, and the concentrations of all forms of carbon in the seawater are in equilibrium with the \(^{14}\text{C}\) tracer. At \(T_0\), the seawater contains labeled \(^{14}\text{C}\), and unlabeled \(^{12}\text{C}\) inorganic carbon, whereas the cell contains only unlabeled organic carbon \(^{12}\text{C}\). As photosynthesis takes place, inorganic carbon is transported into the chloroplast compartment. Within the chloroplast compartment the carbon is converted from inorganic to organic form, and thereby becomes available for transport into the total cell compartment. Both labeled and unlabeled carbon are transported into the chloroplast, but inorganic carbon remains in the chloroplast until it is converted into an organic form. If it is assumed that carbon has not been transported out of the chloroplast, then initially the concentrations of labeled carbon within the two compartments are not in equilibrium.

A comparison of the two compartments would show that the chloroplast compartment contained higher labeled carbon concentrations than the total cell. In time, as progressively more of the inorganic carbon is converted to an organic form and transported into the cell compartment, the ratio of
labeled organic carbon within compartments should approach unity. Once the equilibrium has been established, the minimum time requirement for labeling all cellular carbon pools has been met.

In a phytoplankton cell, however, the transition toward equilibrium is a complicated process. Unlike the conceptual two compartment model, a phytoplankton cell is composed of numerous compartments, all of which are metabolically active. Carbon is transported into and out of all compartments, chlorophyll is synthesized and degraded, and cells divide. Also, external factors influence photosynthesis. Among others, light, temperature, and nutrient availability all influence the rate at which cells photosynthesize.

During the development of the chlorophyll labeling technique, Redalje and Laws (1981) examined the time for phytoplankton to attain equilibrium. Laboratory studies revealed a significant linear relationship between the specific activities of chlorophyll a carbon and total cellular carbon in Thalassiosira fluviatilis (T. weissflogii), based on twelve individual labeling experiments. The minimum incubation period to achieve equilibrium was found to be six hours, with the majority of equilibrium periods twelve hours, or more (Table 1, Redalje and Laws 1981). The conclusion was that chlorophyll a-carbon and total cell carbon are equivalent after a minimum incubation period of six hours. A similar result was reported by Welschmeyer and Lorenzen (1984) during a single time-series experiment with Skeleto-
nema costatum. However in this experiment the first time-series sample was taken after an incubation period of twelve hours.

Field tests of the specific growth method, performed in Kaneohe Bay, Hawaii by Redalje and Laws, consisted of incubations lasting 11.25 h and 11.7 h. Similar incubations lasting 13 h or 24 h, were performed in Dabob Bay, Washington by Welschmeyer and Lorenzen (1984). Neither group of investigators examined the time course of chlorophyll or total cellular carbon labeling in natural populations. The necessary time to establish equilibrium between the activities of chlorophyll carbon and total cellular carbon was inferred from the laboratory data. Inferring equilibrium periods from the laboratory experiments may be unreliable, since the minimum sampling interval in the laboratory experiments was greater than the maximum sampling interval in the field studies. Furthermore, with such long incubation periods, the results may be affected by "bottle enclosure effects", as observed by Gieskes et al. (1979) during long-term productivity incubations.

Redalje (1983) performed further time course studies in both the laboratory and in the Southern California Bight. A time course incubation of Mantoniella sp., in the laboratory, showed that the $^{14}$C activity of total phytoplankton carbon and chlorophyll a-carbon varied in a similar manner after only 2 h. This result showed that not only was equilibrium quickly established, but that it occurred well
before the effects of confinement could be observed.

The papers of Redalje and Laws (1981), Redalje (1983), and Welschmeyer and Lorenzen (1984) taken in toto support the assumption of a rapid cellular equilibrium in phytoplankton. Additionally, an incubation period of between 2 and 12 hours seems sufficient to establish equilibrium between total cellular and chlorophyll carbon.

The recent oceanographic literature indicates that the chlorophyll labeling technique has gained wide acceptance. Studies by Laws et al. (1984) in oligotrophic Hawaiian coastal waters, Gieskes and Kraay (1986) in the open tropical Atlantic, Laws et al. (1987) in the North Pacific subtropical gyre, Taguchi et al. (1988) in the Caribbean Sea and western Atlantic, and Gieskes and Kraay (1989) in eastern Indonesian waters, have all used the chlorophyll labeling technique. Laws et al. (1987) and Taguchi et al. (1988) were the only studies in which time series experiments were performed. The Laws et al. (1987) study included one experiment with a minimum incubation period of three hours, but no conclusion was presented in terms of a minimum labeling time.

Due to the expanding use of the chlorophyll labeling technique, several questions require attention. What are the short-term kinetics in terms of labeling times in different oceanic regimes, and how do these compare? Does the equilibration time vary according to local conditions? And in terms of chlorophyll concentration, what is an adequate
sample size? The answers to these questions will determine how reliably the technique will perform in the open ocean.
Chapter II

Aspects of Phytoplankton Chlorophyll a Carbon-Specific Growth Rate
in the Eastern North Atlantic Ocean
ABSTRACT

A series of time course labeling experiments were performed over a latitudinal gradient extending from 65°N to 8°N, in August, 1988. Experiments were performed during the National Oceanic and Atmospheric Administration (NOAA) Global Change Expedition in the Eastern North Atlantic Ocean to investigate physiological and methodological aspects of phytoplankton growth estimated by the chlorophyll a labeling technique. The objectives were to evaluate the short-term kinetics of the labeling time of natural phytoplankton populations in different oceanic regions, determine the variability of apparent equilibration time in relation to environmental conditions, and compare growth rates from chl a labeling to independent physiological indicators of growth.

The chl a carbon-specific activity ($R^*$) increased during the day at all stations despite differences in day-length, integrated radiation and/or the commencement time of an experiment. The rate of change in $R^*$ increased as a function of decreasing latitude. At stations between 38°N and 20°N rapid short-term increases in $R^*$ were coincident with large increases (> 38%) in the integrated total photosynthetically available radiation (PAR) received between samples. Overestimates in the specific growth rate observed at these stations were explained by the hypothesis that rapid increases in the quantity of PAR received by a phytoplankton cell may result in a disequilibrium between the
activity of the chl a carbon pool and the total cell carbon pool. However, phytoplankton specific growth rates were generally within the limits of empirically-derived temperature-growth estimates, and were strongly correlated with the assimilation number. Apparent equilibration times were short under conditions of low temperature and light (boreal stations), with growth rates becoming constant in as little as two hours. At lower latitudes, as temperature and light increased, growth rates became highly variable during the day. Here, growth rates of samples taken at the end of the day (6.5 - 8.0 hours of incubation) showed the strongest correlation to the average daily growth rate.
INTRODUCTION

Accurate determinations of phytoplankton specific growth rates have, until recently, been constrained by the quality of photosynthetic rate measurements and limitations in determining algal biomass in natural populations. These parameters are determinants of the equation:

\[ \mu = \frac{dC_p}{dt} \times \frac{1}{C_p} \]  

where \( \mu \) \((\text{d}^{-1})\) is the growth rate, derived from \((dC_p \text{ dt}^{-1})\), the photosynthetic rate, and \((C_p)\), the phytoplankton carbon biomass (Redalje and Laws 1981, Redalje 1983). While there is uncertainty in the measurement of photosynthetic rate (Peterson 1980, Harris 1984) there is equal uncertainty in the estimation of carbon biomass (Eppley et al. 1977, Sakshaug 1980). One of the key uncertainties is that current techniques are incapable of separating the phytoplankton carbon fraction from the total particulate carbon.

Redalje and Laws (1981) proposed a method for estimating living phytoplankton biomass by labeling the chlorophyll \((\text{chl a})\) pool with \(^{14}\text{C}\). Since \(\text{chl a}\) is associated with living photosynthetic organisms, isolation and measurement of the \(\text{chl a}\) fraction by chromatography should minimize inaccuracies in the biomass estimate due to non-photosynthetic material. A key assumption of this method is that the specific activities of \(\text{chl a}\) carbon and total cellular carbon are equivalent after the chosen period of isotope labeling (Redalje and Laws 1981, Welschmeyer and
This assumption was tested in the laboratory by studying the time course of labeling in Thalassiosira weissflogii (Redalje 1980, Redalje and Laws 1981), Mantoniella sp. (Redalje 1983), and Skeletonema costatum (Welschmeyer and Lorenzen 1984). The studies indicated that incubation periods of 2 to 12 hours were sufficient to establish an equilibrium between total cellular and chl a carbon. Direct field testing of the assumption has not been possible due to the inability to directly quantify the fraction of living phytoplankton in the total particulate matter (Redalje 1983).

The laboratory evaluation of the validity of the $^{14}$C chlorophyll labeling method has led to a wider use of the technique in recent oceanographic field studies (Laws et al. 1984; Gieskes and Kraay 1986, 1989; Laws et al. 1987; and Taguchi et al. 1988). However, as Redalje (1980) pointed out, "long incubations with natural populations may introduce some amount of error due to possible bottle effects and selective mortality of fragile species during the incubation." Furthermore, he suggested that testing of the chl a technique must be performed with natural populations from different environments to substantiate the assumption that the activity of chl a carbon and total cell carbon are equal.

In view of these suggestions, a series of time course labeling experiments were performed during the National
Oceanic and Atmospheric Administration (NOAA) 1988 Global Change Expedition in the North Atlantic. The time course experiments were designed to investigate both physiological and methodological aspects of the chl a technique with three objectives in mind: first, to evaluate the short-term kinetics of the labeling time of natural populations in different oceanic regions; second, to determine if apparent equilibration time varies with environmental conditions; and third, to compare growth rates determined by the chl a labeling technique to independent physiological indicators of phytoplankton growth.

MATERIALS AND METHODS

Ten time course labeling experiments were performed at stations along the Eastern North Atlantic transect of the (NOAA) Global Change Expedition, aboard the NOAA ship Mt. Mitchell. Figure 1 presents the cruise track and locations of specific growth time course experiments, and Table 1 gives station positions and pertinent information about the physical and chemical environment at each station.

Hydrographic properties of the water column were recorded at each station with a Niel Brown Mark III CTD fitted with a rosette multi-sampler. Water samples for salinity, oxygen, chlorophyll, and nutrient analyses were collected in 2.5 liter Niskin bottles at nine depths on the upcast. A complete summary of station information is given in Frazel et al. (1989).

Nitrate and silicate concentrations were measured in 60
Fig. 1. Cruise track of the 1988 North Atlantic Global Change Expedition. Closed symbols indicate the location of hydrographic stations occupied during the expedition. Open circles indicate the location of time course experiments cited in the text.
Table 1. Station Number, date, geographic position, surface temperature, nitrate, silicate, total photosynthetically available radiation (PAR), and \( \mu \) from end-of-day samples for time course incubation stations occupied during the Eastern Atlantic Leg of the 1988 NOAA Global Change Expedition.

<table>
<thead>
<tr>
<th>Station Number</th>
<th>Date</th>
<th>Lat (N)</th>
<th>Lon (W)</th>
<th>Surface Temp (°C)</th>
<th>Nitrate (µM)</th>
<th>Light (E m(^{-2})d(^{-1}))</th>
<th>( \mu ) (End-of-Day)</th>
</tr>
</thead>
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<tr>
<td>19</td>
<td>8/09</td>
<td>65°44'</td>
<td>29°25'</td>
<td>8.25</td>
<td>8.96</td>
<td>N/A</td>
<td>0.09</td>
</tr>
<tr>
<td>20</td>
<td>8/10</td>
<td>66°38'</td>
<td>28°36'</td>
<td>2.32</td>
<td>0.00</td>
<td>N/A</td>
<td>0.10</td>
</tr>
<tr>
<td>21</td>
<td>8/16</td>
<td>60°00'</td>
<td>20°00'</td>
<td>12.24</td>
<td>2.05</td>
<td>30.57</td>
<td>0.31</td>
</tr>
<tr>
<td>23</td>
<td>8/20</td>
<td>45°57'</td>
<td>20°00'</td>
<td>17.18</td>
<td>0.00</td>
<td>27.20</td>
<td>0.78</td>
</tr>
<tr>
<td>27</td>
<td>8/22</td>
<td>38°01'</td>
<td>19°59'</td>
<td>23.91</td>
<td>0.00</td>
<td>38.62</td>
<td>2.89</td>
</tr>
<tr>
<td>30</td>
<td>8/28</td>
<td>30°28'</td>
<td>30°42'</td>
<td>25.09</td>
<td>0.00</td>
<td>43.12</td>
<td>1.62</td>
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<td>32</td>
<td>8/30</td>
<td>21°12'</td>
<td>34°36'</td>
<td>25.68</td>
<td>0.00</td>
<td>37.29</td>
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<td>16°17'</td>
<td>36°30'</td>
<td>26.47</td>
<td>0.00</td>
<td>45.29</td>
<td>1.41</td>
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<tr>
<td>36*</td>
<td>9/03</td>
<td>08°17'</td>
<td>44°14'</td>
<td>29.03</td>
<td>0.00</td>
<td>43.71</td>
<td>1.01</td>
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<td>38</td>
<td>9/05</td>
<td>11°05'</td>
<td>53°18'</td>
<td>29.14</td>
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<td>42.02</td>
<td>1.81</td>
</tr>
</tbody>
</table>

* Only station with detectable silicate, 0.68 µM.
ml sample aliquots with a four-channel Technicon Auto-Analyzer (Model AA-II). Specific procedures and methodologies for nitrate analysis are described by Armstrong et al. (1967), while silicate analysis followed that of Strickland and Parsons (1972).

Photosynthetically available radiation (PAR) was recorded continuously with a Lambda Instruments 2π quantum sensor, with the spectral response of the sensor limited to the wave-length interval 400-700 nm. Ultraviolet radiation (UV) was also measured continuously using an Eplab UV radiometer. The spectral response of the radiometer was limited to the wave-length interval 295-385 nm. A least squares linear fit of PAR as a function of UV was highly correlated, with \( PAR = UV(206.85) + 97.22 \) (\( r^2 = 0.91, n = 72 \)). This relationship was used to complete missing portions of the PAR data at stations 21, 23, and 27 (Table 1) where the PAR sensor temporarily failed.

Water samples were collected from 5 - 10 m below the surface with a 10 l Teflon-coated Go-Flo bottle attached to a Kevlar-coated hydrowire. The 5 -10 m depth range represented an approximation of the 60% isolume depth. The 60% isolume was chosen since samples from the 100% isolume may be influenced by photo inhibition, while samples from deeper depths were considered more susceptible to light shock.

The Go-Flo bottles were cleaned and rinsed prior to use following the procedures of Fitzwater et al. (1982) to minimize trace metal contamination. All other materials were acid-soaked in dilute (0.1N) BIA HCl, then rinsed copiously
with Milli-Q (18 megohm) water. Incubation bottles were rinsed with the seawater sample before filling. Between experiments the sample bottles were rinsed with dilute BIA HCl and three rinses of Milli-Q water.

Samples from the Go-Flo bottles were collected in 1 l acid-washed clear polycarbonate wide-mouth incubation bottles in a clean van. Samples were inoculated with 0.4 ml of 5 μCi/0.05ml of NAH14CO3 with acid-cleaned Eppendorf pipettes in a clean hood. The isotope (Amersham Searle CFA.3) was prepared in a carrier solution of 0.3 g l−3 BIA grade NA2CO3. Total activities were determined from 0.05 ml aliquots of sample transferred to 0.1 ml of phenethylamine and 3.0 ml Aquasol II scintillation cocktail.

Initial chlorophyll concentrations were determined from duplicate 100 ml aliquots obtained from the Go-Flo bottle and filtered onto Whatman GF/F filters. Filters were frozen over a desiccant at −20°C in the dark. The fluorescence of 90% aqueous acetone extracts was measured in the laboratory using a Turner Designs Model 10 Series fluorometer, after homogenizing the filters and extracting the samples in the dark for 30 min. The fluorometer was calibrated with Sigma chl a, following the method of Smith et al. (1981).

Time course samples were incubated on deck in clear plexiglas cylinders filled with circulating near-surface seawater. The cylinders were covered with neutral density (PVC) screening to simulate the 60% isolume. Time course sub-samples were removed from the incubation cylinders
according to one of two experimental protocols. The first protocol consisted of taking paired sub-samples every 2.0 hours after the start of an incubation until dusk. The object of this design was to assess the reproducibility of the method. The second protocol was to remove one sub-sample every hour after the start of an incubation until dusk. This protocol permitted a finer resolution of labeling patterns.

All sub-samples were transported to the laboratory in the dark. A 100 ml aliquot was removed from the sub-sample and filtered through a Whatman GF/F filter under a pressure differential of < 50 mm Hg for total particulate activity. The GF/F filters were rinsed with filtered seawater such that the surface of the filter was not exposed to air. The filters were then acidified with 0.1 ml of 0.1N HCl and immersed in 3 ml of scintillation cocktail (Aquasol II) (Hitchcock 1986). Sample activity was measured with a Searle Model 300 liquid scintillation counter. The remainder of the sub-sample (900 ml) was filtered through a second Whatman GF/F filter (pressure differential < 50 mm Hg), rinsed with filtered seawater, then immediately frozen in liquid nitrogen for later pigment analysis. Samples were stored in liquid nitrogen until analyzed.

Pigments were extracted and analyzed with chromatography grade chemicals (EM Omnisolv). The frozen samples were homogenized in 90% aqueous acetone (Jeffrey and Hallegraeff 1987). Pigments were extracted in the dark at -5°C for one hour and centrifuged to remove particulates. The clear acetone extracts were decanted into one centrifuge tube
while the particulates remaining in the first tube were re­suspended in 90% aqueous acetone for a second extraction. An ion-pairing agent, Solution P (1.7 g Tetra-n-butyl ammonium acetate and 7.7 g ammonium acetate/100 ml H₂O), was then added to the acetone extract in a ratio of 0.3 ml Solution P:1 ml extract (Mantoura and Llewellyn 1983). The ion-pairing agent enhances the isolation of dephytolated pigments such as chlorophyllide and phaeophorbide (Mantoura and Llewellyn 1983, Bidigare 1985). The mixture was centrifuged in the dark for five minutes to permit binding of the ion­pairing agent. Samples were then injected in a Waters gradient elution HPLC system for pigment separation consisting of a model 680 gradient controller, paired model 501 pumps, and the model U6-K injector.

Pigments were detected by absorbance at 664 nm with a Waters model 481 variable wavelength UV/Vis detector. The signal was plotted and integrated on a Waters model 730 data module (Kleppel et al. 1988). Pigments were eluted over a reverse phase gradient consisting of a 2-solvent mobile phase and a stationary phase. Solvent 1, a solution of water, methanol and Solution P (8:1:1), was mixed with Solvent 2, a solution of methanol and acetone (8:2), in decreasing proportion from 20% Solvent 1:80% Solvent 2, to 100% Solvent 2 over 10 min. Flow rate was simultaneously increased from 1.0 ml min⁻¹ to 1.9 ml min⁻¹ which maintained reasonably constant pressure throughout the gradient. Solvent 2 was delivered at a flow rate of 1.9 ml min⁻¹ an
additional 10 min (Kleppel et al. 1988). The stationary phase consisted of a Beckman C₈ octyl-ultrasphere reverse phase HPLC column (15 cm x 1.5 mm stainless steel; > 40,000 theoretical plates). An octyl-ultrasphere guard column was positioned ahead of the column to reduce contamination of the column. The procedure was repeated for the secondary sample extraction to determine the % chl a recovery.

Chl a and its derivatives were identified by their characteristic retention times (RT) and specific absorption spectra (Table 2). RT's for chl a were initially made from pigment extracts of Thalassiosira weissflogii. RT's for the chl a derivatives phaeophorbide a, phaeophytin a and chlorophyllide a were initially determined from artificially created pigment degradation products (Vernet and Lorenzen 1987). Representative chromatograms of chl a and derivatives are shown in Figure 2.

Chl a fractions from the double extractions were combined in Nalgene filmware bags, evaporated under nitrogen gas, then resuspended in 3 ml of scintillation cocktail (Aquasol II). The specific activity of the chl a fraction was corrected for background and quench as measured with a Searle Model 300 liquid scintillation counter.

The concentration of the chl a fraction was determined by multiplying the area under the chl a peak by a chl a-specific concentration:peak-area ratio, then dividing by the volume of injected extract. The area under the peak is proportional to the pigment concentration (Snyder and Kirkland 1979); and the area varies linearly with pigment con-
Table 2. Chromatographic properties of chlorophyll a and chlorophyll a derivatives.

<table>
<thead>
<tr>
<th>Pigment</th>
<th>Absorption maxima (nm)</th>
<th>RT (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyllide a</td>
<td>436, 664</td>
<td>3.50</td>
</tr>
<tr>
<td>Phaeophorbide a</td>
<td>661</td>
<td>4.88, 8.37</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>432, 665</td>
<td>12.35</td>
</tr>
<tr>
<td>Phaeophytin a</td>
<td>665</td>
<td>13.44</td>
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</table>


Fig. 2. Representative chromatogram of chlorophyll $a$, and chlorophyll $a$ derivatives. Pigment peaks were detected at 664 nm and identified spectrophotometrically by their characteristic absorption spectra. Pigments: 1, unretained fraction; 2, chlorophyllide $a$ and chlorophyll $c$; 3, phaeophorbide $a$; 4, chlorophyll $a$; 5, phaeophytin $a$. 
The concentration:peak-area ratio for chl a was determined by analyzing dilutions of a chl a standard, collecting the chl a fraction as it is eluted, and then measuring its absorbance at 440 nm. Absorbance was measured with an IBM Model 9410 scanning spectrophotometer. The measured absorbance was converted to a concentration estimate with extinction coefficients from Mantoura and LLewellyn (1983).

The chl a carbon-specific growth rate $\mu$ (d$^{-1}$) was calculated from the equation:

$$
\mu = \frac{-\ln [1 - (1.05R^* \times I^*)]}{t},
$$

where $R^*$ (dpm $\mu$gC$^{-1}$) is the specific activity of the chl a carbon, $I^*$ (dpm $\mu$gC$^{-1}$) is the specific activity of the dissolved inorganic carbon, and $t$ (d) is the incubation period as a fraction of the entire day (after Eq. 11, Welschmeyer and Lorenzen 1984).

The variable $R^*$, defined by Redalje and Laws (1981), is derived from the equation:

$$
R^* = \frac{\text{chl a activity}}{\text{chl a carbon} \times (0.7386)}
$$

where the measured chl a activity (dpm) is that of the mass of chl a ($\mu$g) isolated by HPLC. The factor 0.7386 corre-
sponds to the molecular weight of the chl a molecule that is carbon (CRC Handbook of Chemistry and Physics 1981). $I^*$ (dpm $\mu$gC$^{-1}$) was determined by dividing the activity of the seawater sample (dpm l$^{-1}$) by the concentration of inorganic carbon in the seawater ($\mu$gC l$^{-1}$). The inorganic carbon concentration was determined by the method of Parsons et al. (1984).

RESULTS

The chl a concentrations from double extractions of initial time course samples averaged 115% of the fluorometric concentration (coefficient of variation, CV = 0.24, n = 78). Secondary extractions contributed an average of 35% of the total chl a determined by HPLC analyses for all samples (CV = 0.20, n = 78). There was no obvious relationship between either primary or secondary extraction efficiencies and the total chl a concentration.

In general, surface water temperature increased as latitude decreased (Table 1). The coolest surface water temperature, 2.32°C, occurred at 66°N, while the warmest surface water temperatures, ca. 29°C, were found between 11°N and 8°N. Detectable concentrations of nitrate were found only at the northern latitudes, specifically stations 19 and 21. At station 20, the northernmost station (66°N), nitrate was undetectable in the surface waters. Detectable silicate concentrations (0.68 $\mu$M) were found in the surface waters at station 36 (8°N), where surface salinity was 30.81 PSU. PAR (Table 1, column 8), increased with decreasing
latitude, similar to the trend observed for surface temperature. Differences in PAR between nearby stations were attributed to changing meteorological conditions (fog, clouds, rain), whereas larger latitudinal differences were due to changes in both daylength and the maximum light intensity.

Variability in the short-term labeling rate of chl a in relation to geographical location and changing environmental conditions is shown in Figure 3, with PAR and chl a-carbon specific activity ($R^*$) expressed as a function of time of day for stations 23, 30, and 38. Individual data points in Figure 3 and all subsequent figures reflect either a single sample or the sample mean in the case of paired samples. The CV of $R^*$ for paired samples was 0.088 ($n = 13$ pairs). Daylength was approximately 1.0 hour longer in the higher latitudes than in the lower latitudes. The photoperiod started nearly 1.5 hrs later at station 23 (Fig. 3a) in the northern latitudes than at either station 30 or 38 (Figs. 3b, c) in the southern latitudes. Light intensities were higher at stations 30 and 38 (Figs. 3b, c) than at station 23. Maximum intensity was < 1100 µE m⁻²s⁻¹ at station 23, as compared to > 1900 µE m⁻²s⁻¹ at station 38. Higher light intensities accounted for greater PAR at the lower latitudes (Table 1) despite shorter daylengths.

$R^*$ increased during the day at all stations despite differences in daylength, integral radiation and/or the initiation time of an individual experiment. At station 23 (Fig. 3a) a near linear increase in $R^*$ during the incubation
Fig. 3. Photosynthetically available radiation, PAR ($\mu$E m$^{-2}$s$^{-1}$, solid line, starred symbols), and chl a carbon-specific activity, $R^*$ (dpm $\mu$gC, solid line, solid symbols), as a function of time of day (h). (a) station 23, 8/20. (b) station 30, 8/28. (c) station 38, 9/05.
period was strongly related to the increase in PAR. \( R^* = \text{PAR}(36.41) + 24.83, \ r^2 = 0.97 \). A decline in the rate of increase of \( R^* \) at the end of the day relative to the other samples coincided with a decline in light intensity. The increase in \( R^* \) was more variable at station 30 (Fig. 3b). A nearly four-fold increase in \( R^* \) was observed between sub-samples 1 and 2 that coincided with a 50% increase in the total PAR received. Nearly identical \( R^* \) values for sub-samples 2 and 3 coincided with a reduction in light intensity. The \( R^* \) of sub-sample 4 increased relative to sub-samples 2 and 3 although the intensity of light continued to decrease. \( R^* \) and light intensity increased during the incubation period for sub-samples 1 - 3 at station 38 (Fig. 3c). A lower rate of increase occurred with sub-samples 4 and 5 coincident with a decline in light intensity. There was a more pronounced increase in \( R^* \) for end-of-day sub-sample 6 with respect to sub-samples 4 and 5. Here again, the \( R^* \) increased despite decreasing light intensity. PAR, light intensity and the magnitude of \( R^* \) were greater at stations 30 and 38 than at station 23. Highest \( R^* \) values were found at station 30, although highest maximum light intensities were found at station 38.

The temporal variation in \( R^* \) throughout the day at all stations (Figure 4a) was generally linear throughout the day. This occurred irrespective of the time at which an experiment was started. At 6 of 10 stations an increase in \( R^* \) was observed between the first and second sub-samples, although the extent of the increase was not as great as that
Fig. 4. (a) $R^*$ (dpm µgC$^{-1}$) as a function of time of day for all stations. (b) $R^*$ (dpm µgC$^{-1}$) as a function of the change in total particulate activity ($\Delta C$, µg l$^{-1}$) from each incubation bottle. Open symbols denote boreal stations (surface temperatures < 15°C). Closed symbols denote temperate and subtropical stations (surface temperatures > 15°C). Semi-closed symbols denote samples from station 36. Time course stations specifically cited in the text are labeled according to Table 1.
observed between $T_0$ and the initial sub-sample. This observation is important in relation to both the evaluation of minimum equilibration time and accurate determination of growth rate. A decrease in $\mu$ between the first and second sub-samples at all 6 of the affected stations may reflect the variability in equilibration time. The pattern of increase in activity followed by a decrease in activity between the first and second sub-samples was also apparent in the estimates of total particulate activity and the subsequent estimates of primary productivity (see Appendix I).

The increase in $R^*$ as a function of the change in total particulate activity ($R^*:AC$) in Figure 4b shows the variability of labeling in natural populations over a large latitudinal gradient. At boreal stations (open symbols) the $R^*:AC$ ratio is uniformly lower than at southern stations, despite relatively high nutrient concentrations in the surface waters in 2 of 3 boreal stations. At station 20 (66°N) nitrate was undetectable in the upper 30 m. The $R^*:AC$ ratio increased at temperate and subtropical waters as did temperature and light, even as surface nutrients decreased to undetectable concentrations.

The highest $R^*:AC$ values were observed in subtropical waters with no detectable nutrients. A slightly reduced $R^*:AC$ ratio at station 23 occurred in a transition in water masses, from temperate to subtropical waters. Stations to the north of station 23 had water temperatures < 15°C, and salinities < 35.5 psu, while stations to the south had water
temperatures > 23°C, and salinities > 36.2 psu. The $R^*:AC$ values at station 36 were also lower despite being located in subtropical waters. At station 36 silicate but not nitrate was found in the low-salinity surface waters, and, on the basis of T/S characteristics, appeared to be located in a water mass derived from the Amazon-Orinoco River system (Frazel and Berberian 1990).

There was a relatively linear increase in $R^*$ as a function of PAR ($R^*:PAR$) at all stations (Figure 5), with the exception of station 27. A marked difference in the $R^*:PAR$ ratio at station 27 coincided with a doubling of total incident radiation received between sample periods. At the end of the photoperiod a sharp increase in $R^*:PAR$ occurred with the final sample in 5 of 8 stations. Only 8 of 10 stations were considered since light data was not available for the two northernmost stations. In each of the 5 stations with sharp increases the final sample was collected at, or just prior to, dusk. A decrease in $R^*:PAR$ with the final sample in the 3 remaining stations occurred when samples were taken just after dusk. If growth rates were estimated strictly from all day incubations, as will be discussed later, then short-term changes in $R^*:PAR$ at the end of the day may be important. There was no obvious relationship of growth rate to light except for samples where substantial short-term increases in PAR were observed.

Growth rates ($\mu$, $d^{-1}$) increased as a function of the assimilation number ($\text{ANo, mgC mgChl a}^{-1}\text{h}^{-1}$) for all samples, irrespective of the time of day (Figure 6a). Assimilation
Fig. 5. \( R^* \) (dpm \( \mu g C^{-1} \)) of all samples as a function total photosynthetically available radiation (\( \Sigma \text{PAR}, E \ m^{-2} \)). Open symbols denote samples from boreal station 21 (surface temperatures < 15°C). Closed symbols denote temperate and subtropical stations (surface temperatures > 15°C). Semi-closed symbols denote samples from station 36. Starred symbols denote samples from station 30.
Fig. 6. (a) Chl a carbon-specific growth rate ($\mu$, d$^{-1}$) as a function of the assimilation number (ANo, mgC mgChl a$^{-1}$h$^{-1}$) for all samples combined. A least squares linear fit (solid line) to data was $\mu = ANo(0.15) - 0.058$, $r^2 = 0.70$. Open symbols denote boreal stations (surface temperatures < 5°C). Closed symbols denote temperate and subtropical stations (surface temperatures > 15°C). Semi-closed symbols denote station 36, located in a low-salinity water mass. Samples above the dashed line ($\mu > 3.0$) are in apparent short-term isotopic disequilibrium. (b) $\mu$ (d$^{-1}$) from end-of-day samples for all stations expressed as a function of the average daily $\mu$ (d$^{-1}$) for each station. A least squares linear fit (solid line) to data was $\mu - \text{End-of-day} = \mu(0.82) + 0.044$, $r^2 = 0.98$. 
**Figure a**

![Graph](image)

**Figure b**

![Graph](image)
number is considered an independent physiological indicator of growth since chl a values were derived fluorometrically from the initial bottle cast, rather than by HPLC, while productivities were taken from the 100 ml total particulate activity aliquot. A least squares linear fit to all data yielded \( \mu = A\mu(0.15) - 0.06 \) \((r^2 = 0.70, n = 55)\). That the \( r^2 \) explains only 70% of the scatter in this relationship may relate to those samples where \( \mu > 3.0 \). It is suggested below that \( \mu > 3.0 \) may, in fact, be an overestimate due to non-equilibrium among cellular pools. If values of \( \mu > 3.0 \) are excluded, the relationship between \( \mu \) and \( A\mu \) is, \( \mu = A\mu(0.12) + 0.04 \) \((r^2 = 0.81)\). Growth rates determined in end-of-day samples (\( \mu \) end-of-day), i.e. the final sample taken during the photoperiod, was strongly correlated to the mean \( \mu \) calculated from all samples taken throughout the day (Fig. 6b). The relationship from a least squares linear fit was \( \mu \) (end-of-day) = \( \mu(0.82) + 0.044, r^2 = 0.98 \). 

Carbon to chlorophyll (C:Chl) ratios at 7 of 10 stations either remained unchanged, or increased slightly during the day. The temporal change in C:Chl ratios at station 32 (Fig. 7) is typical of stations that showed no change, while stations with increased C:Chl ratios during the day followed a pattern similar to that shown for station 19. At stations 21, 30 and 36, marked decreases in C:Chl were observed during the day. The pattern of decrease in C:Chl at stations 21 and 30 was similar to that shown for station 36 (Fig. 7). The mean C:Chl ratio of pooled samples
Fig. 7. Carbon to chlorophyll a (C:Chl) ratios as a function of time of day for stations 19 (open symbols), 32 (closed symbols) and 36 (semi-closed symbols, dashed lines).
from boreal stations was 306.96, excluding station 21, which showed a significant decline in the C:Chl ratio. In comparison, the mean C:Chl ratio for temperate and subtropical stations (also excluding stations with significant declines) was 163.63, much lower than in boreal waters.

DISCUSSION

Methodology

Initial studies of the $^{14}$C chlorophyll labeling method utilized thin layer chromatographic (TLC) techniques for the isolation of chl a (Redalje and Laws 1981, Redalje 1983, Welschmeyer and Lorenzen 1984). Relatively large volumes of water (ca. 4.0 liters) had to be collected and incubated for this assay to be reliable, particularly in oligotrophic waters. The collection, incubation and filtration of large volume samples is labor-intensive and time consuming. Gieskes and Kraay (1983) and Mantoura and Llewellyn (1983) demonstrated that pigment separation and quantification with high-performance liquid chromatography (HPLC) is both efficient and more sensitive than TLC. Duplicate TLC separations by Welschmeyer and Lorenzen (1984) had an average replication in chl a specific activity of 15% whereas the variation with HPLC was 8.8% in this study. The inherently greater sensitivity of HPLC thus permits smaller sample volumes. The 1.0 liter samples used in this study provided sufficient pigment concentrations for HPLC analysis and permitted rapid filtration of the sample. However, the experimental protocol
of this study called for double pigment extractions on each sample, regardless of pigment concentration. If single extractions had been performed, particularly on samples in oligotrophic waters, an insufficient quantity of chl a would have been eluted by HPLC.

Phaeophorbide a and phaeophytin a concentrations ranging from 3 - 53 ng l\(^{-1}\) were detected at all three boreal stations (stas. 19, 20, 21). The presence of phaeophytin a could be the result of long-term storage, however, samples from other stations analyzed both before and after the boreal stations gave no evidence of detectable degradation products. All samples were stored under identical conditions, in a dewar with liquid nitrogen. Gieskes and Kraay (1983) have reported no detectable pigment degradation when storing samples in liquid nitrogen.

Phaeopigments also result from zooplankton grazing (Shuman and Lorenzen 1975). Phaeophytin a, resulting from acidification of the chl a (Mantoura and Llewellyn 1983), has been attributed to microzooplankton grazing (Law et al. 1988), while the presence of phaeophorbide a has been attributed to macrozooplankton grazing (Welschmeyer and Lorenzen 1985). Since phaeopigments were apparently not due to a storage artifact it is suggested that their presence resulted from zooplankton grazing.

As a methodological consideration, the relatively linear increase in both particulate (Fig. 4a) and chl a (Fig. 4b) activity implies that beginning an incubation after sunrise did not adversely effect the overall experi-
mental results. Similar observations of linear $^{14}$C uptake in natural populations have been demonstrated for a variety of temperatures, seasons and locales (see Glibert et al. 1985, 1986; and Hitchcock 1986), while linear increases in chl $a$ activity have been reported during time-series studies in the North Pacific subtropical gyre (Laws et al. 1987, Fig. 2).

**Chl $a$ Carbon-specific Growth Determinations**

Although the relationship between $R^*$ and $\Delta$C (Fig. 4b) cannot be used to directly test the assumption of labeling equilibrium it is useful for discussing the variability in labeling kinetics in relation to both latitude and environmental condition. The variability in labeling, ranging from low $R^*:\Delta$C at the boreal stations, to high $R^*:\Delta$C at the southern stations, can be modeled in terms of two assumptions. First, it is assumed that $R^*$ represents the labeling of new cell material, and second, that $\Delta$C = $R^*$ + any recycled organic carbon. The recycled carbon pool consists of labeled carbon in metabolic pools other than the chl $a$ pool and/or labeled non-phytoplankton particulate carbon.

At boreal stations (open symbols), uniformly low $R^*:\Delta$C ratios suggest that either the growth rate is extremely low, $^{14}$C is selectively transferred from the chl $a$ pool into other metabolic pools representing an isotopic disequilibrium, or the proportion of non-phytoplankton recycled organic carbon is increasing at a rate faster than the increase of labeled carbon in the chl $a$ pool.
Minor variation in $R^*$ with time (Fig 4a) lends support to the hypothesis that the labeling rate of new cell material was low. Hence, the conclusion that growth rates are low. The selective cycling of $^{14}$C into other phytoplankton metabolic pools is also a possibility, however without specific information on the specific activity of carbon in other pools, such as the protein, or lipid pools, selective cycling of $^{14}$C cannot be accurately inferred. The final alternative suggests that the increase in $\Delta C$ should result from an increase in non-phytoplankton recycled organic carbon.

Apparent zooplankton grazing at the boreal stations, inferred from the presence of phaeopigments, represents a likely mechanism to account for the increase in recycled organic carbon and for the increase in the total particulate activity.

In terms of the higher $R^*:\Delta C$ index at southern stations, increases in growth rate would be predicted if the chl a activity increased at a rate faster than that observed at the boreal stations. If, however, the rate of change in chl a activity were greater than that of the total particulate carbon activity, the result should be an overestimate of the growth rate. In fact, estimated growth rates from sub-samples at stations 27, 30, 32 and 38 exceeded maximum empirical temperature-growth rates of either Eppley (1972) or Goldman and Carpenter (1974). The overestimates could result from errors in the estimation of the fraction of uniform labeling ($L$). $L$, i.e. the % of chl a that is labeled (Gieskes and Kraay 1989), is defined by:
\[ L = 1.05R^* \times I^*-1. \]

where 1.05R* is the chl a specific activity corrected for isotope discrimination and I* is the total dissolved inorganic carbon (DIC) activity (Welschmeyer and Lorenzen 1984).

Welschmeyer and Lorenzen (1984) found that when (L) is high, a small error in (L) can produce disproportionately large errors in the growth rate estimate. Referring to Equation 4, it is assumed that errors would result from the variability of either R* and/or I*. Overestimates of growth rates could be explained in terms of the errors in R* and I*, i.e. in (L), by incorporating the minimum R* (R* - COV) and maximum I* (I* + COV) into equation (2). With this approach all but 3 of the overestimated growth rates still exceed the empirical temperature-growth estimates (Table 3). The overestimate at station 30 coincided with a 55% increase in ΣPAR between samples, while the first overestimate at station 32 coincided with a 38.7% increase in ΣPAR between samples. A secondary instance of high growth rate at station 32 (t = 8.0 hours) coincided with an increase in ΣPAR of only 2.7%. This suggests that the particularly high growth rate at the later incubation period was probably not related to short-term increases in ΣPAR.

The observations that high initial growth rates are related to short-term increases in ΣPAR are consistent with the hypothesis that planktonic algae maintain the ability to adapt to rapid changes in light intensity (Riper et al. 1979). They are also consistent with the observations of
Table 3. Stations in which field estimates of $\mu$ exceed empirical temperature-growth estimates of either Eppley (1972) or Goldman and Carpenter (1974). EPAR refers to the cumulative increase in irradiance at the respective station incubation time.

<table>
<thead>
<tr>
<th>Station Number</th>
<th>Incubation</th>
<th>$\mu_{\text{max}}$ (d$^{-1}$)</th>
</tr>
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<tbody>
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<td></td>
<td>Temp (°C)</td>
<td>Time (h)</td>
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</tr>
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</table>

* Samples which could not be explained in terms of errors in $(L)$. 
Marra and Heinemann (1982) that photosynthesis responds to short-term changes in irradiance (1 - 10 cycles h\(^{-1}\)) rather than integrating the past irradiance history. The fact that \(\mu\) was apparently overestimated during short-term increases in EPAR implies that the assimilation of \(^{14}\)C into the chl a pool occurred at a rate faster than in the total cell carbon pool.

Similar instances of short-term increase have apparently not been reported elsewhere in the scientific literature. However, one apparent instance of short-term increase in \(\mu\) was found in data from Laws et al. (1984). In their Figure 2c, Aug. 30, \(\mu\) increased from 1.27 d\(^{-1}\) to 2.77 d\(^{-1}\) between 9 and 12 hours of incubation. The increase in \(\mu\) is comparable to the observations in this study although light data was not published by Laws et al. (1984) to directly relate \(\mu\) to increases in EPAR.

Despite the apparent overestimation of \(\mu\) at some stations, the overall strong correlation between \(\mu\) and ANo suggests that the chl a labeling method is at the least comparable to another physiological indicator of phytoplankton growth. Studies in the North Pacific (Laws et al. 1987) and Caribbean (Taguchi et al. 1988) showed similar relationships between \(\mu\) and ANo.

The results of this study indicate that differences in environmental conditions, as well as temporal and latitudinal variability observed with respect to chl a labeling make it difficult to specify an adequate minimum incubation
period for all locales. It appears that at boreal stations the requisite incubation period may be as little as two hours. However, at lower latitudes there is so much variability throughout the day that there may not be an appropriate short-term incubation period. The variability of growth rates observed in this study agrees with the conclusion of Redalje (1983), that incubations conducted for a few hours near mid-day could give erroneous estimates of $\mu$ if they are extrapolated to 24 hour rates.

The correlation between average daily, and end-of-day estimates of $\mu$ implies that incubations initiated after sunrise but lasting until the end of the photoperiod appear adequate to facilitate accurate estimates of $\mu$. It is speculated that incubations of from 9 (Gieskes et al. 1986, 1989) to 12 hours (Redalje and Laws 1981, Welschmeyer and Lorenzen 1984, Taguchi et al. 1988) are sufficient to achieve accurate estimates of $\mu$.

It is obvious that there is variability in the short-term labeling kinetics of chl $a$ in natural populations in relation to the temperature and light regime. This variation occurs over large latitudinal gradients in different oceanic regions. As a result, the time required for the activity of chl $a$ and total cell carbon to become equal is variable. Under conditions of low temperature and light, $\mu$ can become constant in as little as two hours. However, $\mu$ becomes more variable throughout the day, as temperature and light increase.

The strong correlation between average daily $\mu$ and $\mu$
end-of-day implies that a full day incubation is probably the best overall incubation period for deriving estimates of \( \mu \) within the present study. Longer incubations (i.e. 24 hours) may also be adequate for estimating \( \mu \) but such inferences fall outside the constraints of the experimental protocol employed in this study. The strong correlation between \( \mu \) and A\(No\) substantiates the view that the chl-a labeling technique is applicable in different oceanic regions under broadly varying environmental conditions.
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CHAPTER III

Distributions of Chlorophyll and Primary Productivity in Relation to Water Column Structure in the Eastern North Atlantic Ocean
ABSTRACT

A meridional transect of stations along 20°W was occupied in August, 1988, during the third leg of the National Oceanic and Atmospheric Administration (NOAA) Global Change Expedition. An additional transect to the south (38°N - 7°N) was occupied to extend the range of latitudinal observations from 60° to 7°N. Latitudinal variations in the megascale (10^3 km) distribution of biological properties were observed in relation to water column structure between 60° and 7°N in the Eastern Atlantic Ocean.

Chlorophyll a concentrations were highest in the northern latitudes (< 2.51 mg m^-3), decreasing to (> 0.2 mg m^-3) in the vicinity of the subtropical gyre, south of 40°N. The nitracline was associated with a shoaling of the pycnocline in the northern latitudes, and the depth of the chlorophyll maximum was associated with the nitracline. At 7°N, high chlorophyll concentrations (ca. 0.5 mg m^-3) were associated with a lens of fresh Amazon River Water. Primary productivity rates were highly variable throughout the transect, ranging from 646.10 mgC m^-2d^-1 to 138.26 mgC m^-2d^-1. Productivity maxima were located south of Iceland, at 46°N (646.10 mgC m^-2d^-1) and in the vicinity of the Azores Front, at 35°N (259.85 mgC m^-2d^-1).
INTRODUCTION

Interactions between physical and biological processes affect the biogeochemical cycling of carbon in the world’s oceans. The extent and form of physical/biological interactions varies both spatially and temporally, and is poorly documented for many oceanic regions. A major goal in modern oceanography is to develop a global understanding of these spatial and temporal relationships. Oceanographic programs, such as the Joint Global Ocean Flux Study (JGOFS) were conceived to investigate global biogeochemical cycles in the ocean. The Global Change Expedition (GCE) also examined the linkage between oceanic biogeochemical cycles and the overlying marine atmosphere. Both programs have included a transect of stations in the Northeastern Atlantic Ocean, along the 20°W meridian, between the Azores and Iceland.

A dominant biological feature along the 20°W meridian (the JGOFS line), as well as the rest of the subarctic North Atlantic, is the annual poleward migration of the spring phytoplankton bloom. The general timing and distributional patterns of the bloom are known, though the underlying physical mechanisms are not as clearly defined [Strass and Woods, 1988]. Studies of Strass and Woods [1988], have documented both the horizontal and seasonal variation of density and chlorophyll profiles in an area adjacent to the JGOFS line, between the Azores and Greenland. The general bloom conditions that they observed have been documented through satellite imagery [Esaias et al. 1986], but a spe-
cific meridional transect to examine the distribution of biological and chemical parameters of the water column along 20°W has not been completed.

The third leg of the National Oceanic and Atmospheric Administration (NOAA) Global Change Expedition included a meridional transect of stations along the JGOFS line in August, 1988 (Figure 1). The objective was to provide a preliminary nutrient and productivity section for comparison with the subsequent Joint Global Ocean Flux Study [Pszenny et al. 1989]. An additional transect to the south (38°N - 7°N) extended the latitudinal observations of the JGOFS line. This paper describes the macroscale (10^3 km) distribution of biological properties and density structure between 60° and 7°N in the Eastern Atlantic Ocean during summer 1988.

METHODS

A total of fourteen hydrographic stations were occupied from 60°N and 7°N (Table 1), between 16 August and 5 September, 1988, aboard the NOAA ship Mt. Mitchell. Between 60°N and 36°N hydro-stations were to be occupied at every 2° of latitude, southward along the 20°W meridian. Hazardous weather conditions encountered after completion of the 60°N station forced the ship to divert to the east of the 20°W meridian. The next hydrostation was therefore occupied at 48°N. South of 36°N, hydrocasts were conducted each morning, without regard to latitude along the cruise track. These stations were generally occupied every 4-5° of latitude.
Fig. 1. Cruise track of the 1988 North Atlantic Global Change Expedition. Closed symbols denote the location of hydrographic stations. Open symbols denote the location of combined hydrographic/productivity stations. Observations from stations 21 to 35 are included in the text.
1988 Global Change Expedition
July 15 - September 6, 1988
Table 1. Station, date, and geographic position of stations occupied during the Eastern Atlantic Leg of the Global Change Expedition.

<table>
<thead>
<tr>
<th>Station</th>
<th>Date</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
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<td>60° 00.0'N</td>
<td>20° 00.0'W</td>
</tr>
<tr>
<td>22</td>
<td>8/19/88</td>
<td>47° 58.8'N</td>
<td>20° 00.0'W</td>
</tr>
<tr>
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<td>8/20/88</td>
<td>45° 57.7'N</td>
<td>20° 00.0'W</td>
</tr>
<tr>
<td>24</td>
<td>8/20/88</td>
<td>44° 00.1'N</td>
<td>20° 01.0'W</td>
</tr>
<tr>
<td>26</td>
<td>8/21/88</td>
<td>40° 02.0'N</td>
<td>20° 00.1'W</td>
</tr>
<tr>
<td>27</td>
<td>8/22/88</td>
<td>38° 01.2'N</td>
<td>19° 59.6'W</td>
</tr>
<tr>
<td>28</td>
<td>8/22/88</td>
<td>36° 01.7'N</td>
<td>19° 59.3'W</td>
</tr>
<tr>
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<td>8/27/88</td>
<td>35° 05.0'N</td>
<td>28° 40.0'W</td>
</tr>
<tr>
<td>30</td>
<td>8/28/88</td>
<td>30° 28.1'N</td>
<td>30° 42.5'W</td>
</tr>
<tr>
<td>31</td>
<td>8/29/88</td>
<td>26° 00.7'N</td>
<td>32° 41.5'W</td>
</tr>
<tr>
<td>32</td>
<td>8/30/88</td>
<td>21° 12.4'N</td>
<td>34° 36.5'W</td>
</tr>
<tr>
<td>33</td>
<td>8/31/88</td>
<td>16° 17.5'N</td>
<td>36° 30.0'W</td>
</tr>
<tr>
<td>34</td>
<td>9/01/88</td>
<td>11° 58.4'N</td>
<td>38° 10.0'W</td>
</tr>
<tr>
<td>35</td>
<td>9/02/88</td>
<td>7° 01.5'N</td>
<td>39° 56.7'W</td>
</tr>
</tbody>
</table>
Hydrographic properties of the water column were recorded at each station with a Niel Brown Mark III CTD, fitted with a rosette multi-sampler. Water samples for salinity, oxygen, chlorophyll, and nutrient analyses were collected in 2.5 liter Niskin bottles at nine depths on the CTD upcast. Sample depths were chosen to cover the depth range of individual hydrocasts. All casts included at least four sample depths down to, and including, 100 m. Three additional samples were obtained in the upper 100 m from stations with Go-Flo bottles (see below). A complete summary of station information is given in Frazel et al. [1989].

Concentrations of inorganic nitrate, nitrite, orthophosphate, and silicate were measured in 60 ml sample aliquots with a four-channel Technicon Auto-Analyzer (Model AA-II). Specific procedures and methodologies for nitrate and nitrite analysis are described by Armstrong et al. [1967]. Orthophosphate analysis follows the procedure of Grasshoff [1965], and silicate analysis follows that of Strickland and Parsons [1972]. Some modifications to these procedures [Technicon Industrial Systems 1976, 1977a, 1977b] were made to enable use of the Auto-Analyzer.

Chlorophyll concentrations were determined from duplicate 100 ml aliquots from each depth filtered through Whatman GF/F filters. Filters were frozen over a desiccant at -20°C in the dark. The fluorescence of 90% aqueous acetone extracts were measured in the laboratory using a Turner Designs fluorometer, after grinding the filters and extract-
ing in the dark for 30 min. The fluorometer was calibrated with Sigma chlorophyll a, following the method of Smith et al. [1981].

Water samples for productivity determinations were collected at three depths with 10 liter Go-Flo bottles mounted on a Kevlar hydrowire. Sampling depths were selected on the basis of light extinction, or on the hydrographic structure of the water column at that station. Due to limited wire time, and the availability of only 3 Go-Flo bottles, samples for productivity incubations at 6 isolumes were obtained from 3 depths. Seawater samples from the shallowest bottle were incubated at 100 and 60% of the incident $I_o$, seawater samples from the mid-depth bottle were incubated at 32 and 17% of the incident $I_o$, and seawater samples from the deepest bottle were incubated at 7 and 1% of the incident $I_o$.

Vertical attenuation coefficients ($k$, m$^{-1}$) were derived at most stations from measurements of photosynthetically available radiation (PAR) obtained by lowering a Lambda Instruments LI-190S 4π spherical collector on the hydrowire. A Secchi disk was used to make an estimation of $k$ when light casts were not performed.

Productivity measurements were made by the carbon-14 method, originally described by Steemann Nielsen [1952], with modifications of Fitzwater et al. [1982] to minimize trace metal contamination. All materials were acid-cleaned in dilute (0.1N) HCl, then rinsed copiously with Milli-Q (18
megohm) water. Incubation bottles were rinsed with the seawater sample prior to filling. Between incubations, sample bottles were rinsed with dilute HCl and three rinses of Milli-Q water. Samples were collected from the Go-Flo bottles in darkened 2 liter acid-cleaned polycarbonate bottles. Approximately 250 ml of sample was transferred to each of three (two light, one dark) acid-cleaned polycarbonate bottles and inoculated with 5 μCi of NaH\(^{14}\)CO\(_3\) with acid-cleaned Eppendorf pipettes. The isotope (Amersham Searle CFA.3) was prepared in a carrier solution of 0.3 g l\(^{-1}\) BIA grade Na\(_2\)CO\(_3\).

The three incubation bottles were encased in elongate tubes of neutral density (PVC) screening simulating 100, 60, 32, 17, 7, and 1% of the incident I\(_o\). Samples were incubated on deck for 4 to 6 hours in clear plexiglas cylinders filled with circulating near-surface seawater. Samples were transported to the laboratory in darkness, filtered through Whatman GF/F filters, and rinsed with filtered seawater without air exposure. Filtrations were performed under a pressure differential of <50 mm Hg to minimize cell breakage [Goldman and Dennett 1985]. The filters were transferred to Nalgene scintillation bags, acidified with 0.5N HCl, and after 60 min. 3 ml of Aquasol II scintillation cocktail was added [Hitchcock 1986a]. Activity was measured aboard ship with a Tracer Model 300 scintillation counter. Productivity (mgC m\(^{-3}\)h\(^{-1}\)) was calculated from the mean value of the two light bottles minus the dark bottle activity.
Hourly integrated productivity estimates (mgC m\(^{-2}\) h\(^{-1}\)) were calculated by trapezoidal integration of individual productivity values at corresponding isolume depths. Daily potential productivity rates were calculated by multiplying the depth-integrated productivity value by a ratio equal to the total light received during the day divided by the light received during the incubation [Hitchcock et al. 1987]. Primary productivity estimates are reported as 'potential' productivity to indicate that while individual productivity estimates were derived from six isolume depths, those samples were not always incubated at the depth from which they were obtained.

Contour maps were generated using a minimum curvature gridding algorithm, employing a ten point quadrant search method. The resultant grids were smoothed by a cubic spline algorithm. Along-track distance was calculated by determining the difference in latitudinal distance between sequential stations, beginning at the northernmost station (60°N).

RESULTS

The distributions of salinity, temperature, density, and silicate are shown for the upper 100 m over a latitudinal extent of 53° (Figure 2). At 60°N, salinities of <35.6 practical salinity units (psu) were observed (Figure 2a). South of 60°N, through the mid-latitudes, surface salinity concentrations increased, with a maximum of >37.2 psu located south of 30°N. The salinity maximum extended to south of
Fig. 2. Isopleths of selected parameters as a function of latitude in the Eastern North Atlantic, August-September, 1988. (a) Salinity, contour interval 0.4 psu. (b) Temperature, contour interval 2°C. (c) Density, contour interval 0.4 \( \sigma_t \). (d) Silicate, contour interval 1 \( \mu \)M. Station locations are denoted by closed symbols across the top of the plot (a).
20°N where the water became less saline. At 7°N a near-surface (5 m) salinity minima was observed (30.76 psu), the lowest salinity observed in the North Atlantic transect. The low-salinity feature extended to 30 m, below which more saline water (>36.0 psu) was present.

A contour map of the isotherm field (Figure 2b) shows a typical increase in water temperature with decrease in latitude. The coolest waters were located at 60°N, where temperatures decreased from 12.4°C at the surface to < 10°C below 70 m. The isotherms deepened south of 60°N. Between 50°N and 40°N a sharp change in the slope of the thermocline is evident at 50 m. The thermocline is less pronounced south of 40°N, where a broad region of relatively uniform temperature (24° - 26°) is located. The region corresponds to the high salinity waters seen in Figure 2a. Krauss [1986] suggests that this area of constant temperature is in the region of the North Atlantic subtropical gyre. The 24°C isotherm shoaled to within 50 m of the surface between 20°N and 10°N, while south of 10°N isotherms deepened. The shoaling of isotherms coincided with the overlying Inter-tropical convergence zone (ITCZ). Highest water temperatures (29°C) were located at 7°N, coincident with the surface low-salinity feature.

A plot of isopycnals (Figure 2c) shows a poleward shoaling and surface outcrop of isopycnal surfaces of increasing density north of (40°N). The highest density at the surface (26.62σt), and at depth (27.29σt, 100 m), were
observed at 60°N. Between 38°N and 33°N, a near-surface density minimum (24.6σt) was found. South of the mid-latitude feature surface density increased (ca. 25.2σt), then decreased to 18.92σt in the low-salinity feature at 7°N. In general the pattern of distribution of isopycnals, other than those associated with the surface salinity minima at 7°N, were similar to the pattern observed for isotherms (Figure 2a).

Detectable levels of silicate (Figure 2d) were limited to three regions within the upper 100 m of the transect. 1 μM concentrations were observed within 55 m of the surface at 60°N. From 60°N to 40°N the 1 μM isopleth deepened to greater than 100 m. From 40°N to 16°N, silicate was not detectable in the surface waters. South of 16°N silicate (1 μM) was observed within 85 m, while at 7°N a silicate maximum of (12.6 μM) occurred at the surface. Also at 7°N silicate concentrations decreased to below 1μM between 40 and 85 m.

The depth of the nitracline (Figure 3a) was associated with a shoaling of the pycnocline (Figure 2c) in the northern latitudes. A plot of nitrate as a function of density (Figure 4) shows that virtually all samples with detectable nitrate occurred at density surfaces between 26.0 and 28.0σt. Near-surface nitrate concentrations of > 2 μM were observed at 60°N (Figure 3a), increasing to > 12 μM below 60 m. In the mid-latitudes, and throughout most of the transect, nitrate levels were below the limit of detection.
Fig 3. Isopleths of selected parameters as a function of latitude in the Eastern North Atlantic, August-September, 1988. (a) Nitrate, contour interval 2 μM. (b) Chlorophyll a, contour interval 0.2 mg m⁻³. Subsurface chlorophyll maxima are denoted by closed symbols. Station locations for both nitrate and chlorophyll are denoted by closed symbols across the top of the plot (a). (c) Productivity, contour interval 0.15 mgC m⁻³h⁻¹. Sample locations denoted by closed symbols.
Fig. 4. Nitrate concentration (µM) as a function of density (σ_t). Closed symbols denote all available observations from hydrographic stations occupied between 60°N and 7°N.
Approaching the latitudes of the ITCZ, detectable nitrate was once again present above 100 m, with 2 μM concentrations within 90 m of the surface.

Highest chlorophyll a concentrations (>1.00 mg m⁻³) were found at 60°N, extending from the surface to 25 m (Figure 3b). South of 48°N chlorophyll concentrations decreased in the surface waters, and south of approximately 40°N chlorophyll concentrations were generally < 0.2 mg m⁻³. The extensive area of low surface chlorophyll concentrations coincides with the subtropical gyre. South of the gyre, near 16°N, the 0.2 mg m⁻³ isopleth shoaled above 80 m, approximately at the latitude of the ITCZ.

The depth of the chlorophyll maximum was not well defined between 60°N and 48°N (Figure 3b, dotted line). However, between 48°N and 40°N a chlorophyll maximum could be identified within the upper 100 m. South of 40°N chlorophyll concentrations increased with depth with no apparent maximum above 100 m. South of 16°N a chlorophyll maximum was once again detectable, shoaling to within 60 m at 7°N.

Productivity stations were occupied at 10 of 14 hydrographic stations, as indicated by open circles in Figure 1. Complete primary productivity results are summarized in Table 2. A contour plot of potential productivity rates as a function of depth and latitude (Figure 3c) shows that highest potential productivity occurred in the northernmost latitudes. South of 35°N, productivity rates were less than one-half the maximum rates observed further north. At 7°N an
Table 2. Station number, depth of the 1% isolume, integrated chlorophyll, integrated primary productivity, assimilation number, and total irradiance during the Eastern Atlantic leg of the Global Change Expedition.

<table>
<thead>
<tr>
<th>Station</th>
<th>1% Isolume Depth (m)</th>
<th>Chl (mg m(^{-2}))</th>
<th>Productivity (mgC m(^{-2})d(^{-1}))</th>
<th>Assimilation Number (mgC mgChl a(^{-1})d(^{-1}))</th>
<th>Total Irradiance (E m(^{-2})d(^{-1}))</th>
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<td>183.36</td>
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</table>


increase in potential productivity near the surface was associated with both the surface low-salinity feature, and a shoaling of the deep chlorophyll maximum.

The integrated daily productivity rate and depth of the 1% isolume (Figure 5) varied as a function of latitude. Highest areal productivity rates (362.46 - 646.10 mgC m\(^{-2}\)d\(^{-1}\)) occurred in the northern waters, and coincided with the shallowest depths of the 1% isolume (19.19 - 38.11 m). Areal productivity rates were generally low though the mid-latitudes (ca. 150 mgC m\(^{-2}\)d\(^{-1}\)) although at 35°N the areal productivity rate increased to 259.85 mgC m\(^{-2}\)d\(^{-1}\), despite deepening of the euphotic zone. The stations at 35°N and 30°N are in the vicinity of the Azores Front [Gould 1985], as such, the observed variability in productivity may be related to the unique water mass characteristics of the frontal zone (see below). South of the frontal region productivity rates decreased to a minimum of 138.26 mgC m\(^{-2}\)d\(^{-1}\) (21°N) then increased toward 7°N.

Assimilation numbers (ANo, mgC mgChl a\(^{-1}\)d\(^{-1}\)) were widely variable, ranging from a low of 9.98 at 60°N to a high of 47.88 at 38°N. This variability was also reflected in a plot of assimilation number as a function of total daily irradiance (Figure 6). A correlation between ANo and irradiance could not be established with samples obtained over such a broad latitudinal gradient.
Fig. 5. Daily integrated potential productivity, mgC m$^{-2}$ d$^{-1}$ (solid line, closed symbols), and depth of the 1% isolume, m (dashed line, open symbols) as a function of latitude.
Fig. 6. Assimilation number, ANo (mgC mgChl a⁻¹d⁻¹) as a function of daily irradiance, I, (Einstein m⁻²d⁻¹).
DISCUSSION

**Phytoplankton Distributions**

Three regions along the transect can be readily defined by their particular T-S characteristics (Figure 7), allowing us to relate the basin-scale distribution of phytoplankton biomass to distinct hydrographic regimes. The transect is divided into a northern region, extending from 60°N to 36°N, a central region, extending from 35°N to 15°N, and a southern region south of 15°N.

Hazardous weather conditions encountered during the survey of the northern latitudes resulted in an extensive interval between 60°N and 48°N in which no observations were taken (Figure 1). To assess the accuracy of contour interpolations performed in this region (Figs. 3 and 4), hydrographic data from August, 1957 and 1958, near 20°W, from Fuglister [1960], were compared with our interpolated observations. Temperature and salinity values from two stations (Station 3838, 58°N, and Station 3857, 52°N) agree well with the interpolated positions of isopleths in Figures 2a and 2b. Fuglister did not calculate density values, but as surface density is primarily a function of temperature and salinity, we consider the latitudinal position of isopycnals (Figure 2c) also to be reasonably accurate.

The poleward transition of surface water characteristics of lower salinity, cooler, high density waters north of 36°N in August-September, 1988 was similar to that reported by Strass and Woods [1988] for an Azores - Greenland tran-
Fig. 7. Temperature-salinity plots for Stations 21 (solid symbols), 28 (starred symbols), and 35 (open symbols).
sector in 1985, although there is some latitudinal variation between the two surveys. From mesoscale (horizontal resolution 14 km) density and temperature observations, Strass and Woods identified the Polar Front at 52°N, as indicated by a temperature increase of 3°C at σ_t = 26.5. We also observed a 3°C change in temperature, and an outcropping of the 26.5σ_t isopycnal, between 60°N and 48°N. However, our data show that surface salinities were greater than 35.0 psu. Hansen and Meincke [1979] used the 35.0 psu isohaline as an indicator of the zone of maximal horizontal gradient, i.e. the Polar Front. The T-S plot of data from 60°N (Figure 6) shows no indication of such a horizontal gradient. As salinity was greater than 35.0 psu, it is therefore suggested that at 20°W, during the time of our survey in August, 1988, the Polar Front was located north of 60°N.

The Polar Front is an important boundary separating biological processes in the Arctic from those associated with the North Atlantic Current. As such, the location of the Polar Front is an important determinant of the spatial distribution of productivity. Strass and Woods [1988] utilized the position of the Polar Front as a means of comparing variations in chlorophyll concentration. They found relatively high mixed-layer chlorophyll concentrations north of the Polar Front, and an even higher subsurface chlorophyll maximum in the relatively oligotrophic waters to the south. We observed a similar mixed-layer chlorophyll maximum in the northernmost waters, and a subsurface chlorophyll
maximum in the more oligotrophic southern waters. However, in contrast to the results of Strass and Woods, mixed-layer chlorophyll concentrations observed to the north were higher than the subsurface chlorophyll concentrations to the south.

There are obvious regional variations that exist in chlorophyll concentrations, both in terms of spatial distributions and year-to-year time scales. Strass and Woods [1988] concluded that the observations of high chlorophyll values were consistent with the prediction from Wood’s [1988] theory of enhanced primary production due to mesoscale upwelling at sites of high isopycnic gradient of potential vorticity. Their conclusions assumed a direct correlation between chlorophyll concentration and primary productivity, since actual primary productivity measurements were not performed. Our coarse scale measures of both chlorophyll concentration (Fig. 3b) and primary productivity (Fig. 5) were generally highest within the latitudes encompassing regions of upwelling, lending further support to the Wood’s theory. Coarse scale upwelling is suggested by the presence of nitrate in both the northern and extreme southern ends of the transect (Fig. 3a), and by the shoaling of isopycnals within those same regions (Fig. 2b).

A schematic of North Atlantic circulation in Krauss [1986, Fig. 19] shows that the central region of our transect (40°N - 15°N) is encompassed by flow about the periphery of the North Atlantic subtropical gyre. Except for the observations at Station 29 (Figure 1), chlorophyll concen-
transitions and primary productivity rates were uniformly low in the region of the central gyre and were comparable to those observed in both the Sargasso Sea [Kiefer and Kremer 1981, Jenkins and Goldman 1985] and in other regions of the North Atlantic subtropical gyre [Jenkins 1982].

The higher values we observed at Station 29 occurred in the vicinity of the Azores Front. The Front was defined by Gould [1985] as the region southwest of the Azores where the depth of the 16°C isotherm shoaled to 200 m. Using this criteria, both Fasham et al. [1985] and Angel [1989] located the Front southwest of the Azores. At our Station 29, the 16°C isotherm occurred between 60 and 80 m [Frazel et al. 1989], while at Station 30, the 16°C isotherm occurred deeper than the limit of the 200 m cast. We assume then, that Station 29 was located north of the Azores Front, in what Fasham et al. [1985] termed Eastern Atlantic Water (EAW), while Station 30 was located south of the Front in Western Atlantic Water (WAW). The position of the Front in relation to Stations 29 and 30 may provide a partial explanation of the latitudinal variability observed in chlorophyll and primary productivity. Our observations of high surface chlorophyll and a shallow chlorophyll maximum in the EAW, and low surface chlorophyll with an underlying chlorophyll maximum assumed below 100 m in the WAW, are consistent with the observations of Fasham et al. [1985, Table 1]. In addition, the observations of higher productivity north of the frontal zone are similar to observations in other fron-
tal regions, including; the shelf/slope region off Nova Scotia [Herman and Denman 1979], the south-eastern United States continental shelf [Yoder et al. 1983], and in the vicinity of the Gulf Stream Front [Hitchcock 1986b].

In the southern region, a comparison of salinity values from bottle samples (measured with a salinometer) with those obtained from the CTD cast at Station 35 confirmed the presence of the low-salinity water at the surface near 7°N. The T-S signature of the low-salinity feature (Figure 7) was similar to the mean T-S curve for a 5° quadrant encompassing Station 5 [Emery and Dewar 1982]. While Emery and Dewar [1982] did not speculate on the origins of these low salinity waters, Ryther et al. [1967] identified its source as Amazon River water. A more detailed analysis of sea surface salinities by Neumann [1969] showed low salinity surface waters occurring over a broad area from 1°N to 10°N and 44°N to 54°W. Considering the mesoscale variability within this region (Fu et al. 1982), it is perhaps not surprising that we observed Amazon River water as far east as 40°W.

The origin of this low salinity water as the Amazon is suggested by the presence of high silicate levels. Both Milliman et al. [1975] and Demaster et al. [1986] have documented the occurrence of high silicate water from the Amazon far beyond the continental shelf. Ryther et al. [1967] reported elevated silicate levels as far east as 50°W, and suggests that their occurrence represents an offshore eddy between the Guiana Current and the North
Equatorial Current. Southerly coastal currents may force such an eddy seaward during a period of slackening, or temporary reversal of the wind system. Both the North Equatorial Current and Guiana Current are under the effect of the Northeast and Southeast Tradewinds [Tchernia 1980], therefore a slackening in winds could, perhaps, permit the offshore movement of an eddy. Ryther et al. [1967] further speculated that the offshore eddy is a regular phenomenon. A recent analysis of NASA coastal zone color scanner (CZCS) imagery by Muller-Karger [1988] shows that these offshore features are a yearly phenomenon, occurring between June and January annually.

From a study of shallow currents along the northeastern coast of South America Metcalf [1968] concluded that the recurving of the high salinity core in the North Brazilian Coastal Current to form the Equatorial Undercurrent permits large lenses of Amazon river outflow to move hundreds of miles offshore.

Spatial Variability in ANo Relationships

The extreme variability in ANo as a function of light (Figure 6) is not unexpected, considering the extensive geographic area that was sampled. Similar variations in ANo - I relationships were observed by Larrance [1971] in the sub-Arctic Pacific. He suggested that the relationship of ANo to daily irradiance in high latitude waters was funda-
mentally different from that in transitional and subtropical waters. For this reason he attempted to relate ANo to I only at stations north of 46°N (Fig. 3, Larrance 1971). The small assimilation number obtained at 60°N (9.88) relative to the high light level is consistent with Larrance's hypothesis of a fundamental difference in ANo - I relationships north of 46°N. The negative correlation between ANo and I at stations south of 46°N may be due to photosynthetic inhibition at the higher irradiances and/or the manner in which estimates of integrated 'potential' productivity were derived. In either case there is still a significant amount of variability over the latitudinal gradient sampled.

Although Balch et al. [1989] showed a positive relationship between ANo and I for data from 648 stations from the Southern California Bight Study, and the California Cooperative Fisheries Investigations, there was a poor correlation between ANo and I ($r^2 = 0.06$). As Balch et al. [1989] pointed out, there is enormous variability in photosynthesis - light relationships in the ocean. The extent of this variability is easily demonstrated from our observations of latitudinal differences in primary productivity in the Eastern North Atlantic.

While remotely sensed data from satellites is being rapidly developed into an important tool for estimating primary productivity on global scales [Brown et al. 1985; Revelle, 1985; Platt, 1986; Campbell and O'Reilly 1987], the estimates must still be ultimately based upon data obtained
from regional shipboard surveys. The observations of regional variations in ANo vs. I relationships for the Northeastern Atlantic in summer 1988 suggest that, as Larrance [1971] initially proposed, there may be a fundamental need for regional studies to develop productivity-light relationships.
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Appendix I
Appendix One consists of the data reports for all specific growth time course stations cited in Chapter Two of the dissertation. Specific growth time course experiments were conducted during the National Oceanic and Atmospheric Administration (NOAA) Global Change Expedition (14 July – 6 September 1988). The Global Change Expedition was a multifaceted research program designed to study atmospheric and oceanic processes affecting the biogeochemical cycles of carbon, nitrogen, and sulfur. Emphasis was on compounds of these elements that may influence the radiation balance of the earth.

The expedition was conducted aboard the NOAA ship Mt. Mitchell in four consecutive legs (Figure 1). The primary objective of Leg I (Norfolk, Virginia – Bermuda) was to examine the potential transport of carbon from nearshore Shelf Water into the Gulf Stream, by means of tracking drogued surface drifters. Leg II (Bermuda – Iceland) was designed to support a survey of the tropospheric chemistry of the North Atlantic. The objective of Leg III (Iceland – Azores) was to occupy a specific meridional transect of stations along 20°W to provide a preliminary nutrient and productivity section for the Joint Global Ocean Flux Study (JGOFS). Leg IV (Azores – Barbados) was similar to Leg III, with nutrient and productivity sampling occurring at dawn each day. This appendix contains data collected at selected stations during legs II, III, and IV. Each data report contains the station date, station position, CTD #, sample
depth. The salinity concentration (practical salinity units, psu) and temperature (°C) were obtained directly from the output of a Neil Brown Mark III CTD.

Chlorophyll a concentrations were determined from duplicate 100 ml aliquots of seawater filtered through Whatman GF/F filters. Filters were frozen over a desiccant at -20°C in the dark. The fluorescence of 90% aqueous acetone extracts were measured in the laboratory using a Turner Designs fluorometer, after grinding the filters and extracting in the dark for 30 min. The fluorometer was calibrated with Sigma chlorophyll a, following the method of Smith et al. [1981].

The specific activity of the dissolved inorganic carbon, $I^*(\text{dpm} \; \mu\text{gC}^{-1})$, was determined from the mean of two 50ul aliquots of sample taken from consecutive sample bottles. The total carbon dioxide present, $W$ (μgC l$^{-1}$) was determined by the method of Parsons et al. (1984).

The procedures for determining the quantity of chl a (ng sample$^{-1}$) isolated, the specific activity of the chl a fraction ($R^*$), specific growth rate (μ), and primary productivity are described in the Materials and Methods section of Chapter Two. Blank spaces are present where time course samples were taken, but not analyzed.
STATION: 80988  LATITUDE: 65°44.50'N  LONGITUDE: 29°25.20'W

CTD #: 19  SAMPLE DEPTH (m): 10  SALINITY (psu): 34.98

I* (dpm⁻¹ μgC⁻¹): 3156.76  W (μgC l⁻¹): 26422.96  Chl a (ng l⁻¹): 970

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I\(^*\) (dpm \(\mu\)C\(^{-1}\)): 3138.07  W (\(\mu\)C l\(^{-1}\)): 26507.87  Chl a (ng l\(^{-1}\)): 2510
STATION: 82088  LATITUDE: 45°57.70’N  LONGITUDE: 20°00.00’W

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I* (dpm µgC⁻¹): 3067.75  W (µgC l⁻¹): 26970.97  Chl a (ng l⁻¹): 400

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Latitude: 11°05.50'N  
Longitude: 53°18.60'W  

CTD #: 53  
Sample depth (m): 5  
Salinity (psu): 34.81  

I* (dpm µgC⁻¹): 2278.4  
W (µgC l⁻¹): 26291.75  
Chl a (ng l⁻¹): 90  

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LATITUDE: 08°17.90'N  
LONGITUDE: 44°14.90'W

CTD #: 36  
SAMPLE DEPTH (m): 5  
SALINITY (psu): 30.76

$I^*$ (dpm µgC$^{-1}$): 2908.01  
$W$ (µgC l$^{-1}$): 23165.79  
Chl a (ng l$^{-1}$): 200

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Appendix II
Appendix Two consists of data reports from all stations cited in Chapter Three of the dissertation. Consecutive hydrographic, nutrient, chlorophyll a, and primary productivity data are given in each report which correspond to the CTD cast, station date, and station position. Methods for temperature, salinity and chlorophyll a (Chl a) concentrations described in Appendix One and Chapter Three of the dissertation. A complete description of the primary productivity sampling protocol and analysis methodology can be found in Frazel et al. (1989).
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CAST: 28  DATE: 82288  POSITION: 36°01.70'N 19°59.30'W

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MASTER REFERENCE LIST


