CARBON UPTAKE AND TURNOVER RATES OF PHYTOPLANKTON IN NEWFOUNDLAND COASTAL WATERS

KEVIN EUGENE PAULEY

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BY

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ABSTRACT

In situ enclosure experiments were completed during phytoplankton bloom and non-bloom conditions in coastal Newfoundland waters. Carbon uptake, pool size and turnover rates of various phytoplankton species and size components were studied using ^{14}C track autoradiography and standard filtration techniques. Total POC was approximately 313 $\mu g\ l^{-1}$ during bloom conditions compared to 188 $\mu g\ l^{-1}$ in the non-bloom enclosure. Approximately 76% of the POC pool in the bloom enclosure was labelled over three days whereas only 32% was labelled in the non-bloom experiment. The measurement of ^{14}C uptake yielded estimates of primary production for bloom and non-bloom conditions in the range of 100 $\mu g\ C\ l^{-1}\ d^{-1}$, which were greater than maximum estimates recorded for the highly productive Grand Banks region (*ca.* 82 $\mu g\ C\ l^{-1}\ d^{-1}$). The measurement of specific cellular carbon uptake over time revealed that, while carbon pool sizes of phytoplankters during bloom conditions agreed well with values found in literature, similar taxa associated with the non-bloom experiment had pools about one half the expected size. Diatoms were responsible for about 51% of the carbon uptake and phytoflagellate nanoplankters 16% during the the bloom. In contrast, nanoplankton accounted for 25% of the non-bloom uptake. The remaining uptake in both experiments could not be attributed to identifiable particulate sources. This suggests that energy flow to higher trophic levels may not be soley through a classical algae-grazer food chain during non-bloom conditions.

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INTRODUCTION

The production of organic carbon by phytoplankton provides the foundation for all major pelagic food webs (Harvey 1955; Steeman Nielsen 1975). In recent years, measurements of oceanic primary production have provided the foundation for the construction of trophodynamic models predicting potential fisheries yield. Nevertheless there is still much debate over the accuracy of the methods used for primary production measurement and the adequacy of the database used for global modeling. In particular there is a paucity of data for many productive marine fishery regions. Agreement between the widely used ^{14}C tracer technique and other procedures such as oxygen measurement have not always been good, and numerous studies have examined the comparability of techniques. Recent research bas also questioned whether measured carbon uptake is always a measure of pbytoplankton growtb, a basic assumption of trophodynamic models.

The present study was designed to obtain accurate measurements of primary production and to relate those measurements to the dynamics of the particulate carbon pool during bloom and non-bloom conditions. The refinement of our understanding of the measurement of carbon flow in marine systems is essential to the implementation of models to predict potential fisheries yields for the inshore waters of Newfoundland. The coastal region is particularly vital because pelagic and benthic fish species use it seasonally as spawning grounds.

The elucidation of carbon flow in the initial step in the food chain, the primary producers, will aid in the prediction of food and energy sources necessary for the successful recruitment of larval fish in coastal waters. The early estimation of recruitment into the commercial fishery could provide much-needed stock management advice without using the hindsight of catch per unit effort evaluations. The use of trophodynamically-based potential fish yields in a-

rigorous management role could allow the continued propagation of socially and economically valuable fisheries.

1.1. MARINE PRODUCTIVITY

The ability to measure very low levels of primary production was enhanced with the development of the ^{14}C tracer technique by Steeman Nielsen in 1952. As information on global marine primary production proliferated, attempts were made to collate the available data. Koblentz-Mishke *et al.* (1968) assigned specific levels or ranges of productivity to different parts of the oceans; rates of primary production were observed to vary by at least two orders of magnitude. Ryther (1969) estimated potential fish production based on global primary production and trophic efficiency estimates, and suggested that most fisheries were already being exploited at or near their potential maximum. Over-exploitation can rapidly lead to failure of a fishery and consequently to major socioeconomic and social disruption. The importance of more accurate primary production estimates for future fishery production evaluations is thus apparent.

The Canadian Atlantic continental shelf region supports one of the world's most productive fisheries, yet few studies of primary productivity have been conducted there (Hollibaugh and Booth 1981). Akenhead (1980), Anderson (1980), Anderson and Gardner (1988), and Hill *et al.* (1973) have made measurements of primary productivity in the Grand Banks continental slope region. Mills and Fournier (1979) used primary production estimates to formulate a trophodynamic model for the evaluation of estimates of potential fishery yield on the Scotian Shelf and were unable to account for the observed fishery yields with the low levels of primary production measured. A similar observation has been made in the offshore waters of the Grand Banks (Hollibaugh 1981). To date, no researchers have addressed the question of primary production and its relationship to fisheries production in the inshore waters of the Grand Banks. This uncertainty about absolute values of biological productivity is true for vast tracts of the world's oceans (Smith *et al.* 1984).

1.2. PRIMARY PRODUCTION METHODOLOGY

Cushing *et al.* (1958a) define primary production as "the carbon fixed per m^2 or per m^3 per unit time". Radioisotope uptake was first used as a sensitive means to measure aquatic primary productivity by Steeman Nielsen (1952) and has since become the principal method used to determine primary productivity in coastal and oceanic environments (Davies and Williams 1984). The use of the ^{14}C tracer to measure primary production has been augmented by many alternate approaches, such as changes in ATP (Sheldon and Sutcliff 1978), changes in dissolved oxygen (Tijssen 1978), and changes in particle number and volume (Sheldon *et al.* 1973).

Peterson (1980), in a thorough review of ^{14}C methodology, noted that while very close agreement has often been found between ^{14}C and traditional light/dark bottle oxygen techniques, numerous discrepancies still remain. Davies and Williams (1984) indicated several potential sources of variation, including methodological bias, containment effects, and different sampling and incubation strategies. The problems associated with the measurement of primary production using tracer techniques have frequently been addressed in the literature.

The flow of labelled carbon through the photosynthetic system into short and long-term end products has received considerable attention recently (Morris 1980; Li and Harrison 1982; Barlow 1984b; Welschmeyer and Lorenzen 1984; Palmisano and Sullivan 1985; Sargent *et al.* 1985). The incorporation of label into a variety of products such as proteins, carbohydrates, pigments, lipids, and a variety of intracellular carbon pools has been documented to vary with the length of incubation. Since some of these end products, such as lipids, do not indicate growth, variation in length of incubation can yield data that become difficult to interpret. Productivity is often measured during short term ^{14}C incubations, on the order of 2 to 6 hours, a period which is usually shorter than the division time of the population. As a consequence, carbon fixation during the incubation period may not be directly coupled to cell growth.

1.2.1. INCUBATION TECHNIQUES

Production estimates can vary depending on the portion of the photoperiod used for the incubation. Disagreements between primary production estimates can therefore be observed when the results of short-term incubations are compared to those of long-term ones (Harris 1978; Morris 1980; Peterson 1980). Although short-term incubations generally yield higher primary production estimates than long-term ones it is thought that longer incubations are more likely to include any cyclic patterns of carbon or nutrient uptake (Venrick *et al.* 1977; Goldman 1980; Morris 1980). The containment of phytoplankton for long-term incubations does, however, present many potential physiological problems which could yield low estimates of primary production.

In order to maintain long-term incubations (>4 hrs), "bottle" or "containment" effects must be minimized. Some of the effects of containment in incubation bottles include: photo-inhibition (Goldman and Dennett 1984), nutrient limitation (Hattori *et al.* 1980), phytoplankton death (Venrick *et al.* 1977), and trace metal contamination (Davies and Williams 1984). Trace metal contamination of both incubation containers and/or ^{14}C stock solutions has been shown to cause inhibition of photosynthesis during incubations (Geiskes *et al.* 1979; Carpenter and Lively 1980; Fitzwater *et al.* 1982). Many containment effects can be attributed to the size of the vessel in use. Gieskes *et al.* (1979) found that the rate of decrease in chlorophyll, interpreted as an undesirable containment effect, was an inverse function of container size. Containers holding more than 4 liters do not appear to enhance phytoplankton mortality (Geiskes *et al.* 1979), and Parsons (1982) suggests that more trophic levels can be examined as container size is increased.

Parsons (1981), and more recently Banse (1982), have both provided historical reviews of the use of enclosures to conduct plankton research *in situ*. Strickland and Terhune (1961) pioneered the use of large plastic enclosures to study multi-species or natural marine plankton assemblages *in situ*. The types of enclosures currently in use for such studies vary from dialysis cultures (Shultz and Gerhardt 1969; Jensen *et al.* 1972) and cage enclosures (Owens *et al.* 1977;

Sakshaug and Jensen 1978), to free-floating pelagic ecosystems (a further refinement of the plastic bag idea) that can hold as much as 1700 m^3 (Menzel and Case 1977). The main advantages of such large enclosures are that they allow the study of discrete parcels of water and their associated communities for extended periods of time while allowing the manipulation of variables such as nutrients, light, and pollutants. Although Parsons *et al.* (1977) suggest that enclosures lack small scale physical turbulence, there are containments such as flexible polyethylene tubes which at least partially overcome this (Eppley *et al.* 1978). Ichimura *et al.* (1980) used an enclosed water column to determine ^{14}C productivity per unit area.

Kuiper *et al.* (1983) have documented concurrent phytoplankton blooms inside and outside *in situ* plastic enclosures, indicating that events inside the enclosures reflect those which occur naturally. Goldman (1962), Menzel and Steele (1978), and Kuiper (1982) have all utilized large, flexible, translucent bags to enclose natural plankton communities. Kuiper *et al.* (1983) compared enclosures, ranging between 1 and 30 m^3, in the Rosfjorden fjord, Norway, and found that the 1-2 m^3 volumes were sufficient to avoid "bottle" effects and permit long-term (4-8 wk) incubations of phytoplankton. Total plankton communities can be contained in larger enclosures (15 m^3) under nearly natural conditions for extended periods of time (4-6 wk: Jahnke *et al.* 1983). By avoiding the containment problems often found in simulating natural environments within the laboratory, *in situ* experimentation can be extrapolated more reliably to open sea conditions (Jahnke *et al.* 1983).

1.3. CARBON UPTAKE VS GROWTH

The question of whether the ^{14}C method measures net or gross primary productivity rates remains a problem. Growth can be measured as the change in biomass via cell counts or as changes in particulate organic carbon (POC). Early concepts of growth and primary production (Steeman Nielsen 1952) suggested the two processes may be synonymous: however, studies by Barlow (1984b) and Li and Harrison (1982) found that newly incorporated carbon was directed to cell

components such as photosynthetic pigments and lipids, which are not always good indicators of growth. Smith (1982) also suggested that the proportion of carbon in any one of these components or pools which is metabolically active may vary. High rates of carbon pool turnover do not necessarily result in phytoplankton growth. For example, organisms utilizing a small proportion of their cell carbon pool in rapid recycling would produce a high carbon flux but not necessarily an increase in biomass (Smith 1982). The size of the metabolically active carbon pools in a natural phytoplankton population needs to be determined on a species level to understand carbon flow better in marine phytoplankton communities. Boulding and Platt (1986), Douglas (1984), and Smith *et al.* (1984) have all addressed the topic of carbon uptake by various portions and size fractions of phytoplankton communities but their techniques have not permitted a description of carbon uptake by individual taxa within of marine phytoplankton communities.

There has been a recent movement from the community level to the organismic level to understand the fundamental processes of primary production and carbon flow better in marine systems. The traditional use of ^{14}C tracers for community production estimates has been modified for examination of individual phytoplankton community components. Knoechel and Kalff (1976) developed ^{14}C track autoradiography as a method for the determination of phytoplankton species productivity in freshwater, and this approach is being applied to oceanic systems as a part of the Plankton Rate Processes in the Oligotrophic Oceans (PRPOOS) study to increase understanding of carbon turnover rates and pathways.

1.4. RESEARCH OBJECTIVES

My project was designed to determine rates of primary production in Newfoundland inshore waters and to address the inconsistencies currently being encountered with respect to ^{14}C incorporation and population growth estimates. Carbon uptake, pool size, and turnover rates of various phytoplankton species and size-components were examined for phytoplankton populations using ^{14}C track

autoradiography as well as standard filtration techniques. The experiments were conducted in (1 m^3) *in situ* enclosures to minimize containment effects and to avoid extrapolations from laboratory phytoplankton cultures grown in artificial environments.

MATERIALS AND METHODS

To elucidate the patterns of carbon flow in marine phytoplankton, 1 m^3 polyethylene enclosures were deployed in both phytoplankton bloom and non-bloom conditions in coastal Newfoundland waters. These long-term (100 hr), *in situ*, time course incubations allowed a detailed observation of primary production and carbon flow on both a species and community level.

2.1. STUDY AREAS

The spring bloom enclosure experiment was conducted in Bonne Bay, a fjord located on the west coast of Newfoundland (Figure 2-1). This site was choosen because of its relatively easy access in early spring, its sheltered nature, and the laboratory facilities offered by the adjacent Memorial University field station at Norris Point (Lat. 49° 31' 00" N, Long. 57° 52' 10" W). The bloom enclosure was deployed from 1-5 May 1984, when surface water temperature was 6 °C with a thermocline at 10 m. At this time of the year, the upper portion of the water column represents a combination of winter-cooled Labrador current water and Labrador current water (I. Webster, pers. comm.).

The non-bloom enclosure experiment was conducted during 20-26 July 1984 in a small cove of Logy Bay (47° 37' 30" N, Long. 52° 40' 00" W), located just northeast of St. John's Newfoundland and adjacent to the Memorial University Marine Sciences Research Laboratory (Figure 2-1). Preliminary experiments were also conducted at this site during 21-23 May and 14-15 September 1983. Logy Bay is strongly influenced by Labrador current water (LCW) flowing south from Labrador over the Funk Island Banks. This water, before its introduction onto the continental shelf, is characterized by temperatures of -0.5 to -1.0 °C and salinities of about 33 parts per thousand. During the summer, warm air

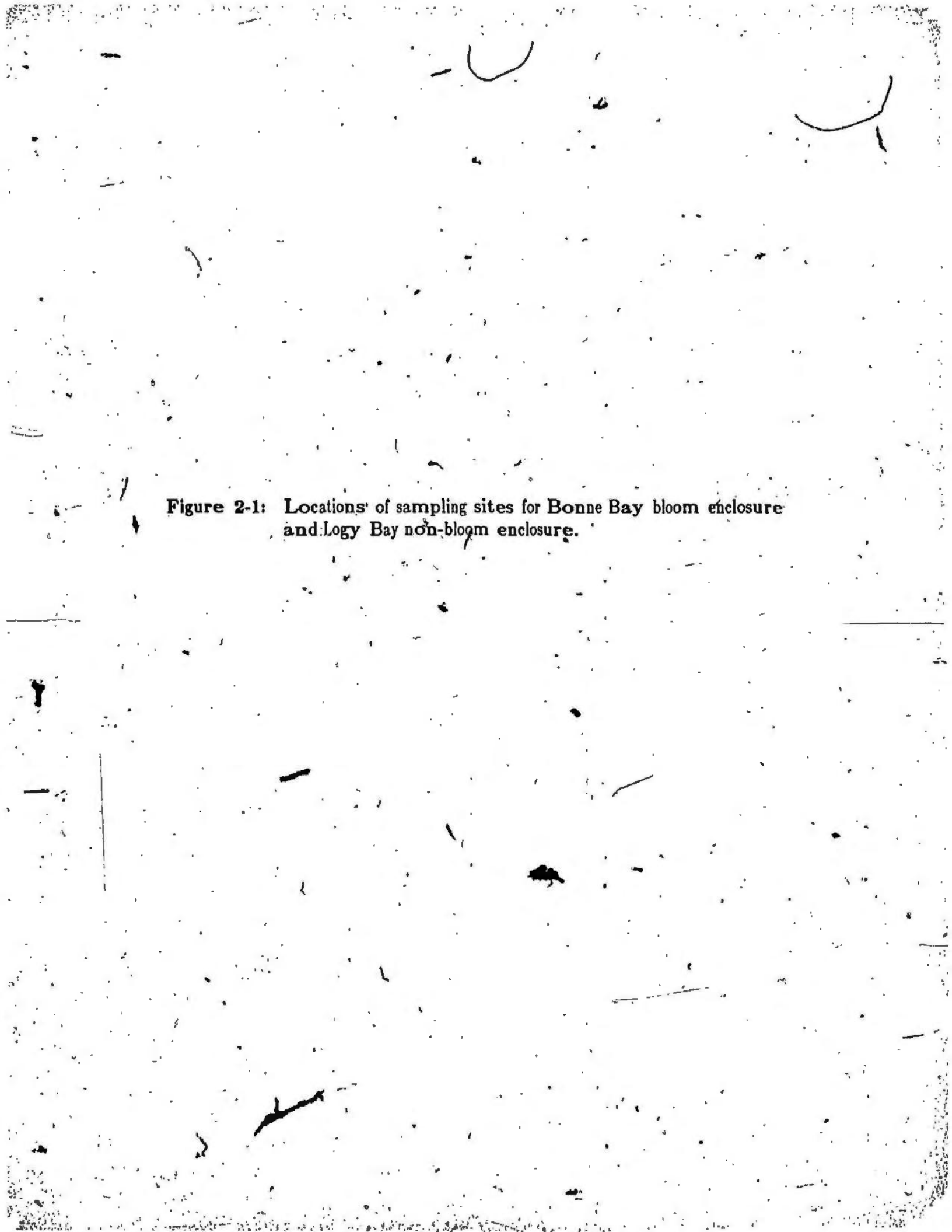
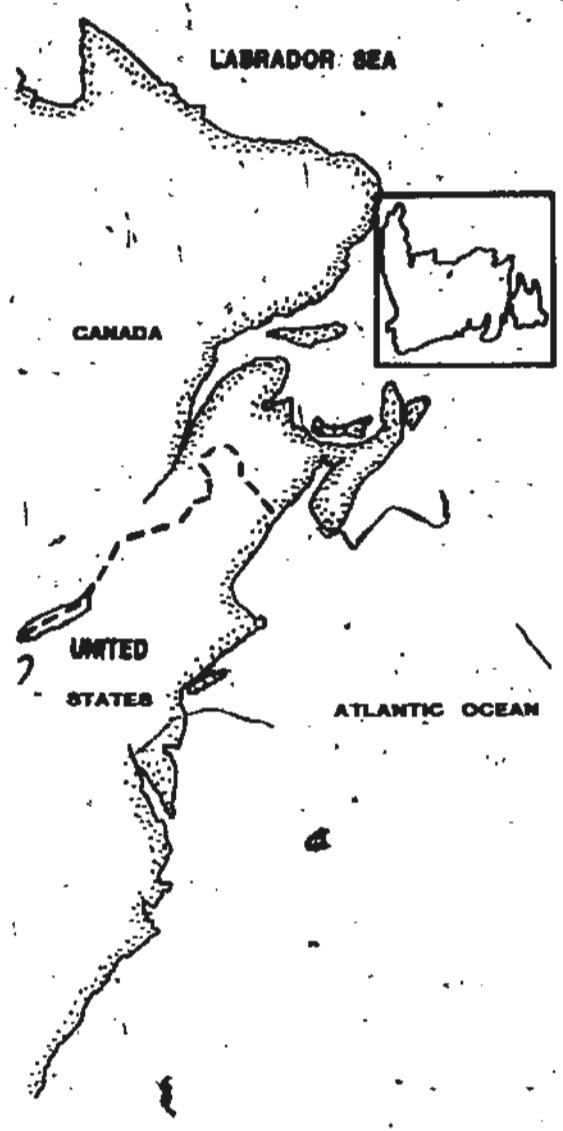
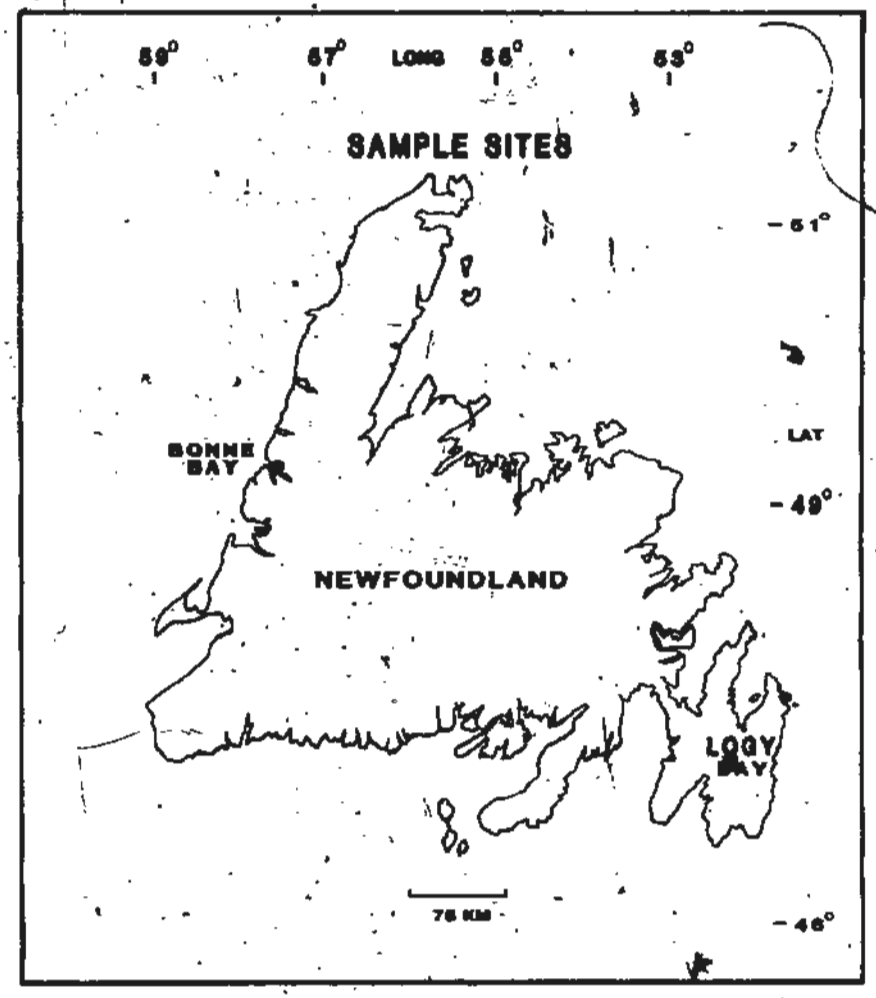


Figure 2-1: Locations of sampling sites for Bonne Bay bloom enclosure and Logy Bay non-bloom enclosure.


LABRADOR SEA
CANADA
UNITED
STATES
ATLANTIC OCEAN


59°
57°
LONG
55°
53°
SAMPLE SITES
51°
LAT
49°
BONNE BAY
NEWFOUNDLAND
LOGY BAY
75 KM
46°

temperature, high insolation, and fresh water runoff modify the LCW and coastal waters can become stratified. Water temperature was a uniform 14.5 °C to a depth of 12 m during the non-bloom experiment. Prevailing summer winds from the west and south-west can generate along-shore currents that lead to periodic upwelling of deeper, unmodified Labrador current water.

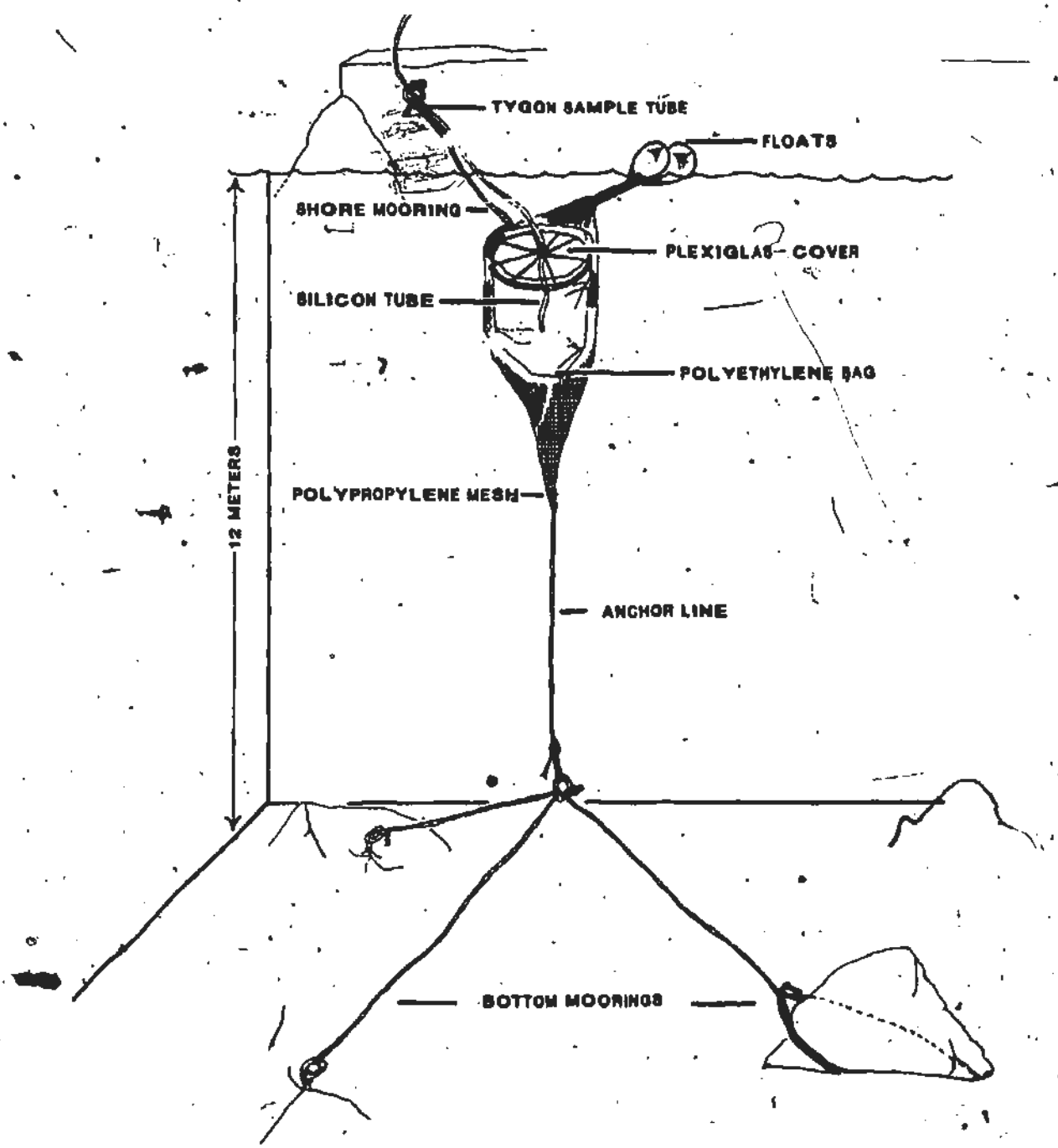
2.2. BAG CONSTRUCTION

The enclosures for primary production experiments were constructed of 1 m diameter polyethylene tubing (0.25 mm thickness) which was cut and heat sealed to hold a volume of 800-900 l. Heat-sealed seams were reinforced on the outside of the bag with clear, 5 cm wide plastic tape. The top support for the bag was constructed of 8 Plexiglas supports glued between two 1 m diameter discs made of 3 mm Plexiglas (Figure 2-2). A band of 3 mm Plexiglas was glued around the edge to seal the cover shut. Air spaces left between the supports provided buoyancy, while nylon hose fittings screwed into the center of the cover provided a sampling and inoculation port. Two of these supports were constructed and submerged in Logy Bay for approximately 2.5 months to allow leaching of any toxins that may have been present in the Plexiglas. Polyethelyene tubing (Tygon, 7 mm i.d.) used for sampling was pushed onto the outside cover fitting and secured with a metal hose clamp. A piece of silicon tubing (7 mm i.d.) was attached to the inside fitting so that samples were drawn from the approximate center of the enclosure.

2.3. MOORINGS

The experimental enclosures were moored at sites selected by inspection of areas using S.C.U.B.A.. The enclosure in Bonne Bay was moored to an abandoned anchor chain. In Logy Bay, a much more exposed site, the enclosure was attached to a triangular mooring arrangement made up of ring bolts driven into bedrock and steel cables attached to a boulder (Figure 2-2).

Figure 2-2: Illustration depicting deployment of enclosure for *in situ* sampling.


TYGON SAMPLE TUBE
FLOATS
SHORE MOORING
PLEXIGLAS COVER
SILICON TUBE
POLYETHYLENE BAG
POLYPROPYLENE MESH
12 METERS
ANCHOR LINE
BOTTOM MOORINGS

2.4. DEPLOYMENT OF BAG

Bags were deployed by S.C.U.B.A. divers operating from an inflatable boat. Deployment took place in late afternoon to minimize the amount of photosynthetic activity within the bag before inoculation with the ^{14}C tracer. The bag was folded and lightly taped to avoid premature filling. Two divers took the bag to a depth of approximately 10 m, where it was unfolded and pulled towards the surface with the mouth held open. At the surface, the plexiglas cover was secured in the bag opening by a stainless steel hose-clamp. A temporary sample tube was placed on the cover for inoculation purposes and clamped shut to prevent water leakage from the bag. The bag was then enveloped in 18 cm polypropylene mesh (Otter trawl net material), which was sewn closed by divers with net mending needles and twine. Floats were attached to the mesh near the cover to identify the apparatus as a navigation hazard should it break free from its moorings. The bag was positioned over the moorings (Figure 2-2) at a depth of approximately 0.5 m by the boat crew and secured to the central mooring shackle by divers. The enclosure was also moored to the shore with 9 mm nylon-polypropylene rope, which also provided support for the sampling tube attached to it at 3 m intervals.

2.5. INOCULATION OF BAG

The bags were inoculated with 1 mCi of $NaH^{14}CO_3$ based on the results of two preliminary studies carried out at the Logy Bay site in 1982-83 to determine optimum tracer activity. The inoculation was done after dark to permit thorough mixing before daylight. The radioisotope was drawn into a disposable 50 cc syringe and injected into the bag via the temporary short sampling tube. The inoculum was then chased with approximately 2 l of sea water to insure that the tubing was sufficiently flushed. The temporary sampling tube was removed and the permanent enclosure-to-shore sampling tube was connected and secured with a metal hose clamp.

2.6. SAMPLING

Water samples for analysis of primary production, phytoplankton identification and enumeration, and determination of total seston were removed from the bags at 2-3 hr intervals (Table 2-1) using a vacuum pump powered by a 600 watt portable electric generator. Water was collected in a 4 l borosilicate glass vacuum flask. A full flask of water (4 l) was drawn and discarded to flush the sampling tube with the equivalent of five volumes before the sample was collected. Two 100 ml flint glass bottles were filled with sample water at the collection site and immediately preserved with acid Lugols, for later use in phytoplankton enumeration and identification, ^{14}C autoradiography, and preserved particulate organic ^{14}carbon ($PO^{14}C$) estimation. The remaining water was transported back to the laboratory where subsamples were taken to determine dissolved inorganic ^{14}carbon ($DI^{14}C$), particulate organic ^{14}carbon ($PO^{14}C$), total particulate organic carbon (POC), particulate organic nitrogen (PON), and chlorophyll *a* (Chl *a*).

In the laboratory, duplicate 5 ml $DI^{14}C$ samples were taken using an automatic pipette and placed in 20 ml polyethylene scintillation vials (Fisher) containing 10ml of scintillation cocktail (*Aquasure*, New England Nuclear) previously buffered to pH 9.5 to prevent loss of tracer as carbon dioxide. $PO^{14}C$ was collected from duplicate 200 ml water samples filtered through glass microfibre filters (2.54 cm Whatman GF/C) and placed in 20 ml polyethylene scintillation vials with 1 ml of 0.5 N HCL to drive off inorganic ^{14}C (Lean and Burnison 1979). Samples were allowed to sit for 24 hr prior to the addition of scintillation cocktail (*Aquasure*, 10 ml). Total organic carbon ($TO^{14}C$) concentrations were determined from single 10 ml aliquots of Lugols-preserved water samples. The 10 ml sample was placed in a 20 ml polyethylene scintillation vial and 50 μl of 1 N HCl was added to liberate inorganic carbon as CO_2. Sodium thiosulfate solution (20% aq., 20 μl) was added to decolour the samples and CO_2, in the form of dry ice, was added to the samples twice at 24 h intervals to insure sufficient gas liberation via bubbling. Scintillation cocktail (*Aquasure*, 10 ml) was then added and the samples were allowed to stand overnight before counting.

Table 2-1: Example of sampling schedule for field collections.

	TIME (HR)	ACID LUGOLS 2 x 100 ML	POC / PON 2 x 400 ML 2.5 cm GF/C	CHL *a* 2 x 1 L 4.7 cm GF/C	TOTAL DIC-14 2 x 5 ML **	POC-14 2 x 200 ML 2.5 cm GF/C + 1 ML .5N HCL*
	0500	X	X	X	X	X
	0700	X			X	X
	0900	X	X	X	X	X
Day	1100	X			X	X
1	1300	X	X	X	X	X
	1500	X			X	X
	1700	X	X	X	X	X
	1900	X			X	X
	2100	X	X	X	X	X
	2400	X	X	X	X	X
	0300	X			X	X
	0500	X	X	X	X	X
	0700	X			X	X
Day	1000	X	X	X	X	X
2	1300	X			X	X
	1600	X	X	X	X	X
	1900	X			X	X
	2100	X	X	X	X	X
	2400	X	X	X	X	X
	0300	X			X	X
	0500	X	X	X	X	X
	0700	X			X	X
Day	1000	X	X	X	X	X
3	1300	X			X	X
	1600	X	X	X	X	X
	1900	X			X	X
	2100	X	X	X	X	X
	2400	X	X	X	X	X

** PLUS 10 ML OF BUFFERED AQUASURE SCINTILLATION COCKTAIL
* PLUS 10 ML OF AQUASURE SCINTILLATION COCKTAIL

PO^{14}C was also determined for 100 ml aliquots of Lugols-preserved samples filtered through glass microfibre filters (GF/C 2.54 cm Whatman) and placed in 20 ml polyethylene scintillation vials with 10 ml of *Aquasure* scintillation cocktail. These samples provided a measure of total community production for comparison with autoradiographic estimates of activity in individual taxa, which were performed on preserved samples. All filtering was performed under a vacuum of less than 120 mm of mercury.

Total particulate carbon and nitrogen samples were collected from duplicate 400 ml water samples filtered through pre-combusted glass microfibre filters (450 °C for 1 h, 2.54 cm Whatman GF/C). The filters were folded in half, sample side in, to avoid loss of particulates, and then wrapped in pre-ashed aluminium foil and stored at -20 °C.

Chlorophyll *a* was determined from duplicate 1 l water samples filtered through 4.7 cm Whatman glass microfibre filters (GF/C). These filters were also folded in half, sample side in, and frozen at -20 °C prior to processing.

2.7. SAMPLE PROCESSING

2.7.1. AUTORADIOGRAPHY

Track autoradiography techniques, used to determine carbon uptake at the cellular level, supplied estimates of carbon flux for specific phytoplankton taxa. Slides for autoradiography were prepared from 10 ml aliquots of Lugols-preserved water using settling chambers previously described by Knoechel and Kalff (1978). The slides were rinsed with distilled water (saturated with I_2 to inhibit bacterial growth) to remove salt and non-particulate ^{14}C. Cells were allowed to settle 4 d before the first rinse, a period determined to be sufficient to settle even small cyanobacteria. Six subsequent rinses were done at 24 hr intervals, the last with a 100 mg l^{-1} gelatin solution, which provided a suitable base for adhesion of the nuclear emulsion. The slides were air dried for approximately 30 hr. Replicate slides were dipped in nuclear emulsion (Kodak, NTB3) and exposed for periods of 2-22 d to produce a suitable range of track densities for cells of varying activity.

The slides were then processed following Knoechel and Kalff (1976), with development for 8 min at 20 °C. Slides were prepared for observation by mounting a coverslip with 30% glycerin.

Tracks, defined as a string of at least four silver grains arising within 5 μm of a cell, were counted on an Olympus BH-2 phase contrast microscope. Cells were located under phase contrast at 450x and then tracks were counted at 900x using the wrong phase ring to reduce visual interference from the cell. Estimates of new carbon per cell were made using the equation described by Knoechel and Kalff (1976):

$$\text{Carbon cell}^{-1} = \frac{tracks(cells \cdot exposure)^{-1} \times 2.0}{0.86 \times 0.98 \times 60 \cdot (min \cdot hr^{-1})} \times \frac{DI^{14}C}{DI^{12}C}$$

where tracks is the total number of tracks counted, cells is the total number of cells counted, exposure is the length of time the slide was incubated in hours, $DI^{14}C$ is the total activity of isotope in the enclosure (discentegrations per minute), and $DI^{12}C$ is the available dissolved inorganic carbon which was assumed to be 24 mg C l^{-1} (Sandeman and MacLagen unpub.). The factor 2.0 corrects for the geometry of the detector, in which half of the disintegrations enter the slide and are not detected, the 0.86 factor corrects for the 14% of the beta particles with insufficient energy to produce a four grain track (Levi and Rogers 1963), 0.98 corrects for 2% self-absorption by the labelled cell (Knoechel and Kalff 1976), and 60 converts the tracks per hour data into tracks per minute form for comparison with the $DI^{14}C$ activity.

2.7.2. POPULATION ESTIMATES

Preserved phytoplankton samples were examined to determine species composition and abundance, both of which were essential to the elucidation of species specific carbon fluxes and contributions to the $PO^{14}C$ pool. Phytoplankton were settled on glass slides, as previously described, for identification and enumeration. Three rinses were found to be adequate during the settling process to remove excess salt. After drying, a glass coverslip was mounted in 1-2 drops of freshly prepared 30% glycerin and sealed with nail polish

to prevent evaporation. Organisms were observed and counted at 450x or 900x using an Olympus BH-2 phase contrast microscope and converted to cells ml^{-1} by correcting for the initial volume of water each field represented. Phytoplankton were identified based on descriptions by Butcher (1959, 1967), Manton and Parke (1960), Hendey (1964), Brunel (1970), and Lackey and Lackey (1970).

2.7.3. RADIOISOTOPE MEASUREMENT

Radioactivity of $PO^{14}C$, $TO^{14}C$, preserved $PO^{14}C$, and $DI^{14}C$ samples, was determined by liquid scintillation counting using a Beckman LS3150T liquid scintillation spectrophotometer. All vials containing scintillation cocktail were kept in the dark prior to counting to avoid the induction of photoluminescence. Means of 6 replicate 10 minute counts were corrected for efficiency using the external standard ratio technique calibrated with an internal ^{14}C-toluene standard. Carbon fixation was calculated as:

$$\text{Sample activity} \times \frac{DI^{12}C}{DI^{14}C}$$

where $DI^{12}C$ is the dissolved inorganic carbon present (*ca.* 24 mg C l^{-1}, Sandeman and MacLagen unpub.), and $DI^{14}C$ is the dissolved inorganic radioisotope activity in the sample. The carbon fixation in the $TO^{14}C$ component of the carbon pool was determined by substituting the appropriate $TO^{14}C$ values for the sample activity values in the above equation.

Leakage of tracer from the bag during the course of the experiments was corrected for by multiplying the carbon fixation data by the ratio of the initial $DI^{14}C$ to the measured $DI^{14}C$ for that sample time. Estimates of maximum carbon incorporation (carbon pool size) were determined as the level at which saturation of POC with labelled carbon was observed.

The rate of carbon pool labelling was examined in terms of carbon pool turnover time for comparison with rates of cell growth determined from changes in cell abundance. The turnover time of carbon pools in bloom and non-bloom enclosures was calculated by fitting a saturation model, using least squares

regression, to the respective curve using the equation described by Welschmeyer and Lorenzen (1984):

$$L = 1 - (2^{-kt})$$

where L is the ratio of carbon label at time t to the maximum amount of carbon in the carbon pool, k is a rate constant, and t is the time in photodays. The turnover time describes the time it takes for the entire pool to be replaced, at which point it would be 50% labelled (after two turnovers the pool would be 75% labelled, after three 87.5%, ...).

2.7.4. PARTICULATES

Levels of seston, measured as particulate carbon and nitrogen, were determined to estimate the size of the community carbon pool and to provide estimates of biomass in each of the enclosures over time.

Particulate carbon and nitrogen concentrations were measured using a Perkin-Elmer Model 240 elemental analyzer. Desiccated filters were wrapped in 3 cm square pieces of pre-ashed aluminium foil prior to combustion in the analyzer. Both blank filters and acetanylide standards were processed while running samples to insure that measurements were accurate. The coefficients of variation for C and N standards were 0.1% and 0.4% respectively. Atomic C:N ratios were calculated for both bloom and non-bloom enclosures as an indicator of phytoplankton condition.

2.7.5. CHLOROPHYLL

Concentrations of chlorophyll *a* determined during bloom and non-bloom periods and were used both as indicators of containment effects and as an estimate of the living portion of the seston, when coupled with corresponding measurements of POC. Chlorophyll *a* concentrations were determined on acetone extracts by fluorometry (Strickland and Parsons 1972). The filters were ground manually with a teflon tissue grinder in 10 ml of 90% acetone, capped and kept in a dark refrigerator for a minimum of 1 hr. The extract was filtered through

Whatman #1 qualitative paper filters and read on a 10-005R Turner Designs Model 10 Field Fluorometer. The fluorometer was calibrated by comparing fluorometer values with measures of natural marine phytoplankton pigments using a Bausch & Lomb spectronic 210UV spectrometer. Concentrations of chlorophyll *a* were calculated using the phaeophytin corrected equations described in Strickland and Parsons (1972).

2.7.6. CELL CARBON ESTIMATES

Potential carbon cell^{-1} estimates were needed for comparison with the labelled carbon pool size estimates based on track autoradiography. The plasma volume to cell carbon conversion suggested by Strathman (1967) was used for diatoms. Cell volume was also determined for phytoplankton cells to estimate total phytoplankton biomass. Plasma volumes were estimated by measuring area (μm^2) from scale drawings of the cells in question and assuming a plasma thickness of 3 μm. A computerized digitizer was used to carefully measure plasma areas from scale drawings of cells with irregular shapes. The potential carbon content of other types of cells were calculated from the carbon:volume relationship described by Strathman (1967).

C: Chl *a* ratios were monitored over time as an indicator of containment effects and phytoplankton physiological condition. The amount of phytoplankton carbon present in the seston was estimated from chlorophyll *a* data using published C:Chl *a* ratios (Goldman [illegible] Hollibaugh and Booth 1981; Valiela 1984). C:Chl *a* ratios from my data were calculated for comparison to the above data by dividing the POC (μg C l^{-1}) by the corresponding concentration of Chl *a* (μg Chl *a* l^{-1}).

2.7.7. STATISTICS AND GRAPHICS

The relationship between the ^{14}C activity in preserved and non-preserved POC samples collected on filters was examined using the least squares regression method as described in Sokal and Rohlf (1969). The standard error of track

counts for autoradiography-based carbon uptake rates were calculated using tables of Crow and Gardner (1959), because the data conform to a Poisson distribution. Standard errors for POC, PON, chlorophyll *a*, and cell abundance were all calculated as described in Sokal and Rohlf (1969).

The SPSSX^{TM} and SPSS^{TM}Graphics systems (SPSS Inc. 1983) were used in the processing and graphic representation of data.

RESULTS

3.1. SESTON

Total seston levels, measured as POC, remained stable over time in both experiments, with that in the bloom being approximately twice that in the non-bloom enclosure. The mean POC concentration in the bloom enclosure was 313 $\mu g\ l^{-1}$ as compared to 188 $\mu g\ l^{-1}$ in the non-bloom enclosure (Figure 3-1; data in Appendices A and B). Agreement between duplicates was poorer for the non-bloom data (Figure 3-1), as indicated by a lower coefficient of variation in the bloom enclosure (CV= 11.9% in bloom and CV= 14.0% in non-bloom), perhaps due to the incidence of rare, very large particles (*i.e.* detritus, diatom colonies). The PON data were similar in botb experiments, with mean levels of 29 and 24 $\mu g\ l^{-1}$ in the bloom and non-bloom enclosures respectively (data Appendices A and B). Linear regression of POC and PON with time showed no significant relationship in either the bloom or the non-bloom enclosures (POC: p= 0.59 and p= 0.71; PON: p=0.11 and p= 0.78 respectively).

Ratios of carbon to nitrogen (atomic C:N) are often used as a reflection of phytoplankton condition. Redfield *et al.* (1963) suggested that healthy phytoplankton cells growing in logarithmic growth phase in laboratory cultures should have a C:N ratio of approximately 7, with higher ratios generally indicating nitrogen deficiency. Atomic C:N ratios were relatively high in both enclosures, 13.11 $\pm$1.07 and 9.25 $\pm$0.58 for the bloom and non-bloom experiments respectively, indicating probable nutrient stress.

Chlorophyll *a* (Chl *a*) concentrations recorded in the bloom enclosure were approximately four times those observed in the non-bloom experiment, with mean levels of 1.14 $\mu g\ l^{-1}$ and 0.27 $\mu g\ l^{-1}$ respectively (Appendix C). The greater between experiment variation in Chl *a* concentration (four-fold) as compared to

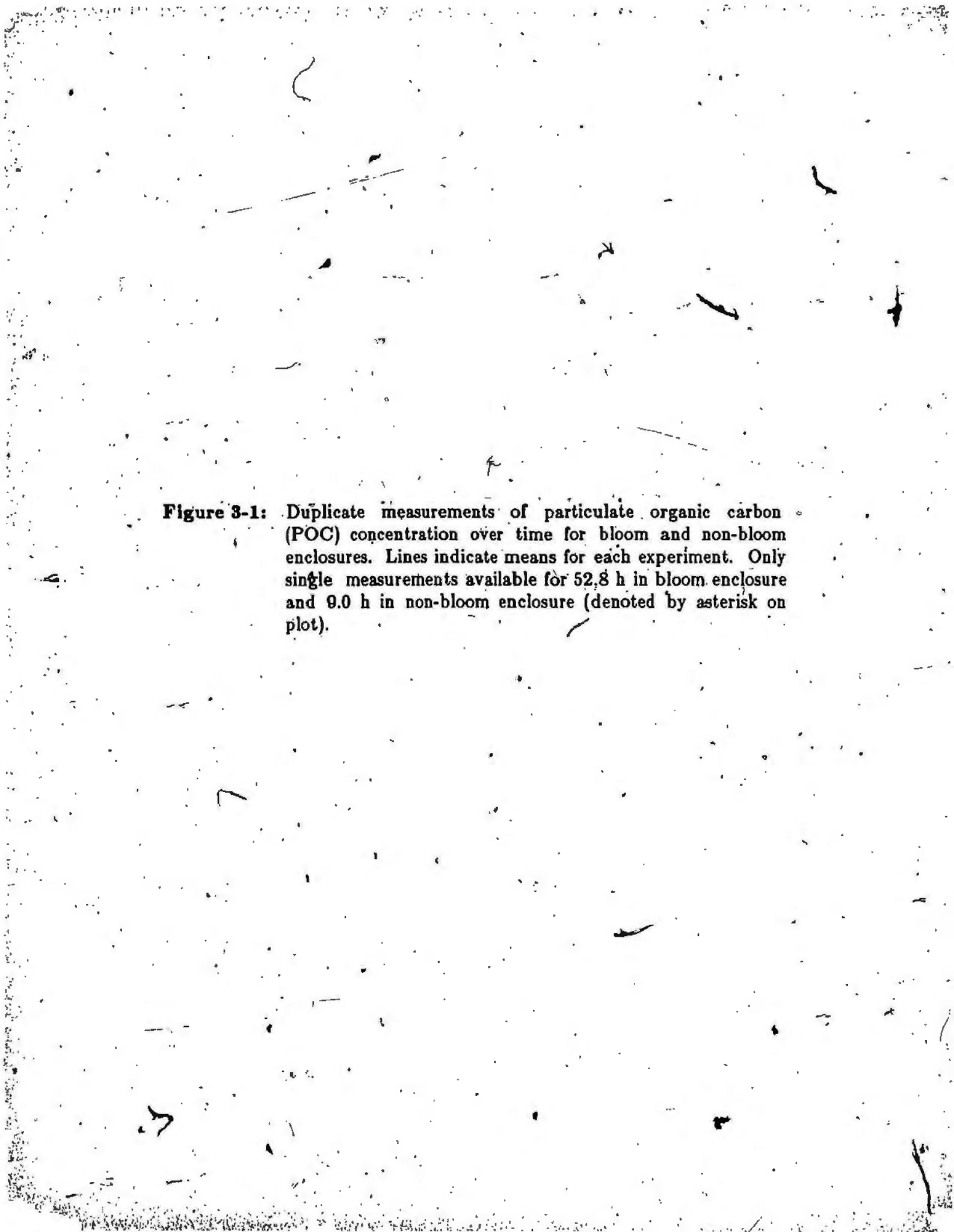
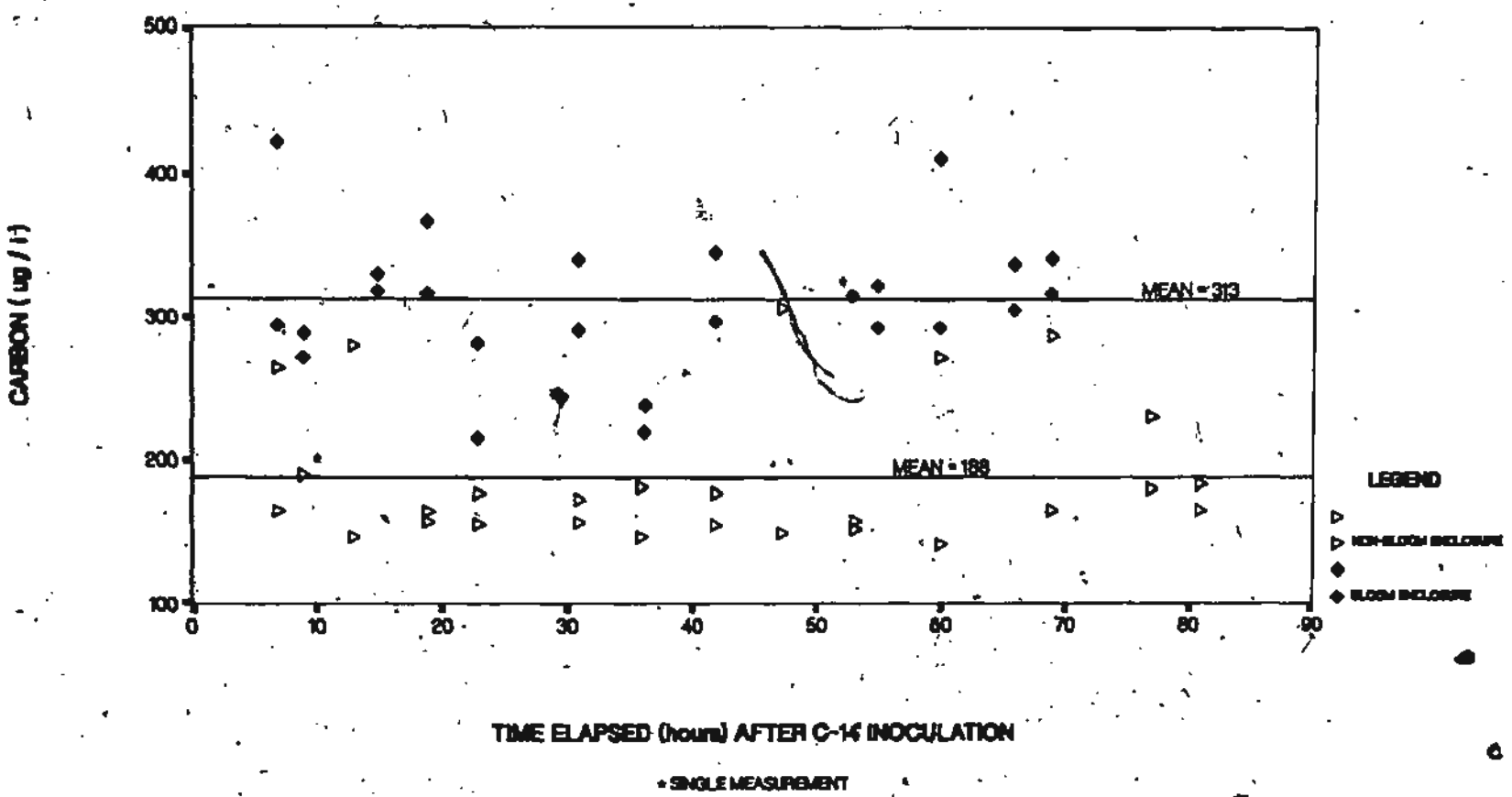


Figure 3-1: Duplicate measurements of particulate organic carbon (POC) concentration over time for bloom and non-bloom enclosures. Lines indicate means for each experiment. Only single measurements available for 52.8 h in bloom enclosure and 9.0 h in non-bloom enclosure (denoted by asterisk on plot).

POC CONCENTRATION OVER TIME FOR BLOOM AND NON-BLOOM ENCLOSURES

Duplicate measurements



POC concentration (two-fold) suggests that a larger portion of the non-bloom seston was made up of non-living or detrital material. Microscope observations of settled particulates on slides confirmed this. There was a statistically significant increase in Chl *a* over time in the bloom enclosure ($p = 0.003$, Figure 3-2), while the non-bloom level remained stable over the 3 day incubation period ($p = 0.96$, Figure 3-3). Linear regression of Chl *a* with time indicated an increase in Chl *a* of 0.19 $\mu g\ l^{-1}\ 24\ h^{-1}$ in the bloom enclosure. The absence of significant decrease in Chl *a* concentrations over the full incubation periods in both bloom and non-bloom enclosures can be used as evidence for lack of containment effects (Geiskes *et al.* 1979).

The ratio of POC to Chl *a* has been used as an indicator of phytoplankton fitness and physiological condition. Low C:Chl *a* ratios (40-60) are representative of phytoplankton cultures in logarithmic growth, while nutrient deficient conditions lead to an increase in the ratio to a maximum of approximately 150 (Valiela 1984). Steele and Baird (1965) note that ratios above 150 are often recorded in natural populations because detritus levels can be high enough to influence the POC estimate. Ratios of carbon to Chl *a* (C:Chl *a*) calculated for bloom and non-bloom enclosures showed a decreasing trend in the bloom enclosure ($p = 0.09$), with values ranging from 541 downward to 214 over time. This trend was expected as the average POC level did not appear to change while the Chl *a* concentration did significantly increase. No significant relationship with time ($p = 0.78$) was noted in the non-bloom experiment, with values ranging from 1605 to 331 (Figure 3-4) over the course of the incubations.

The high seston C:N and high C:Chl *a* ratios, and the presence of diatom resting spores (see below), suggest that the phytoplankton in both experiments were nutrient stressed and thus likely had cellular C:Chl *a* ratios at the high end of the scale. Multiplying the Chl *a* concentrations observed by C:Chl *a* ratios ranging from 50 and 150 (minimum and maximum observed in cultures) should yield minimum and maximum estimates of the proportion of sestonic POC which was living phytoplankton. The peak estimates of the living portion of seston on the final day of incubation, using a ratio of 150, suggested that at most 65% of

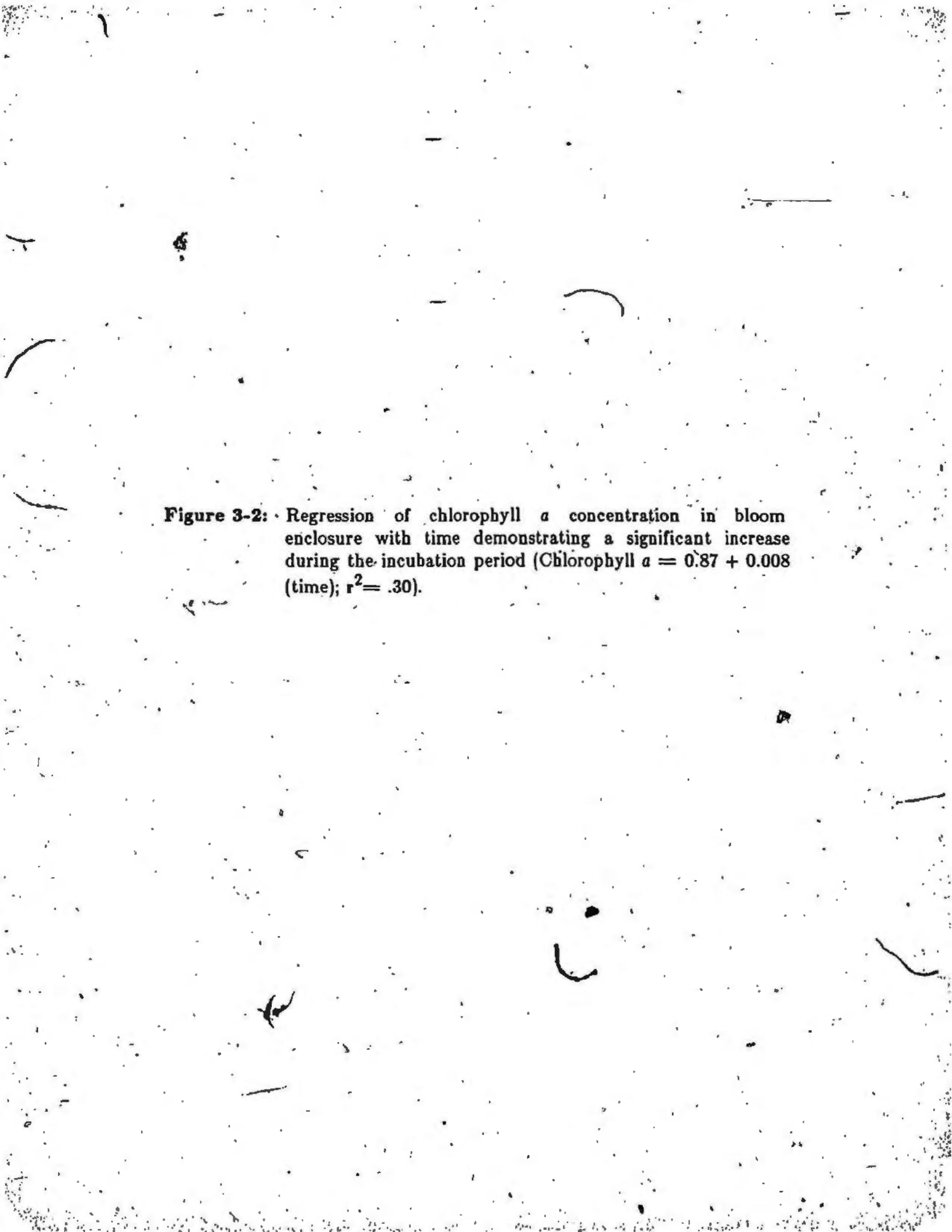


Figure 3-2: Regression of chlorophyll *a* concentration in bloom enclosure with time demonstrating a significant increase during the incubation period (Chlorophyll $a = 0.87 + 0.008$ (time); $r^2 = .30$).

REGRESSION OF CHLOROPHYLL A CONCENTRATION IN BLOOM ENCLOSURE WITH TIME

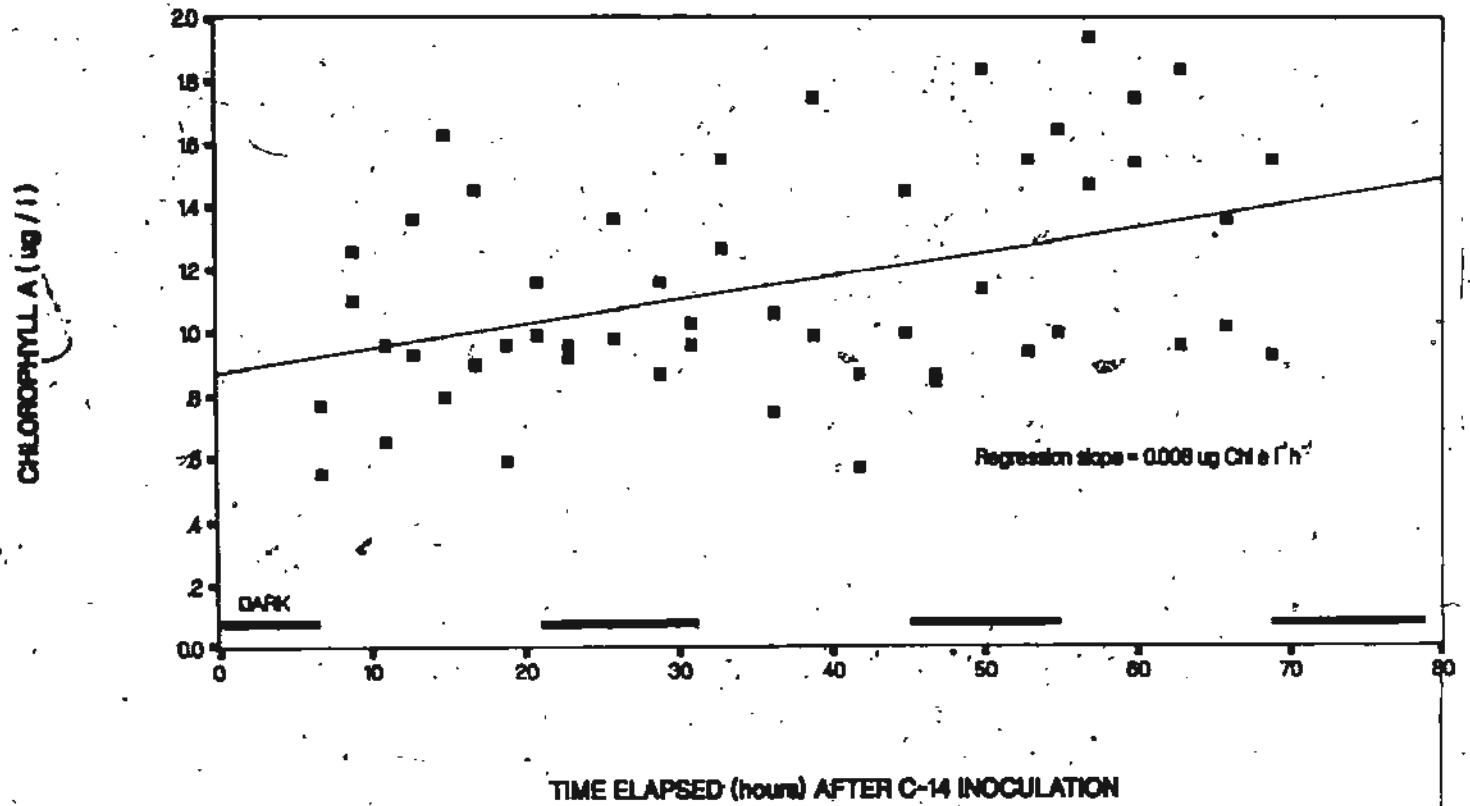


Figure 3-3: Plot of chlorophyll *a* concentration over time for non-bloom enclosure. No significant increase was observed over the incubation; horizontal line indicates mean concentration.

CHLOROPHYLL A CONCENTRATION OVER TIME FOR NON-BLOOM ENCLOSURE

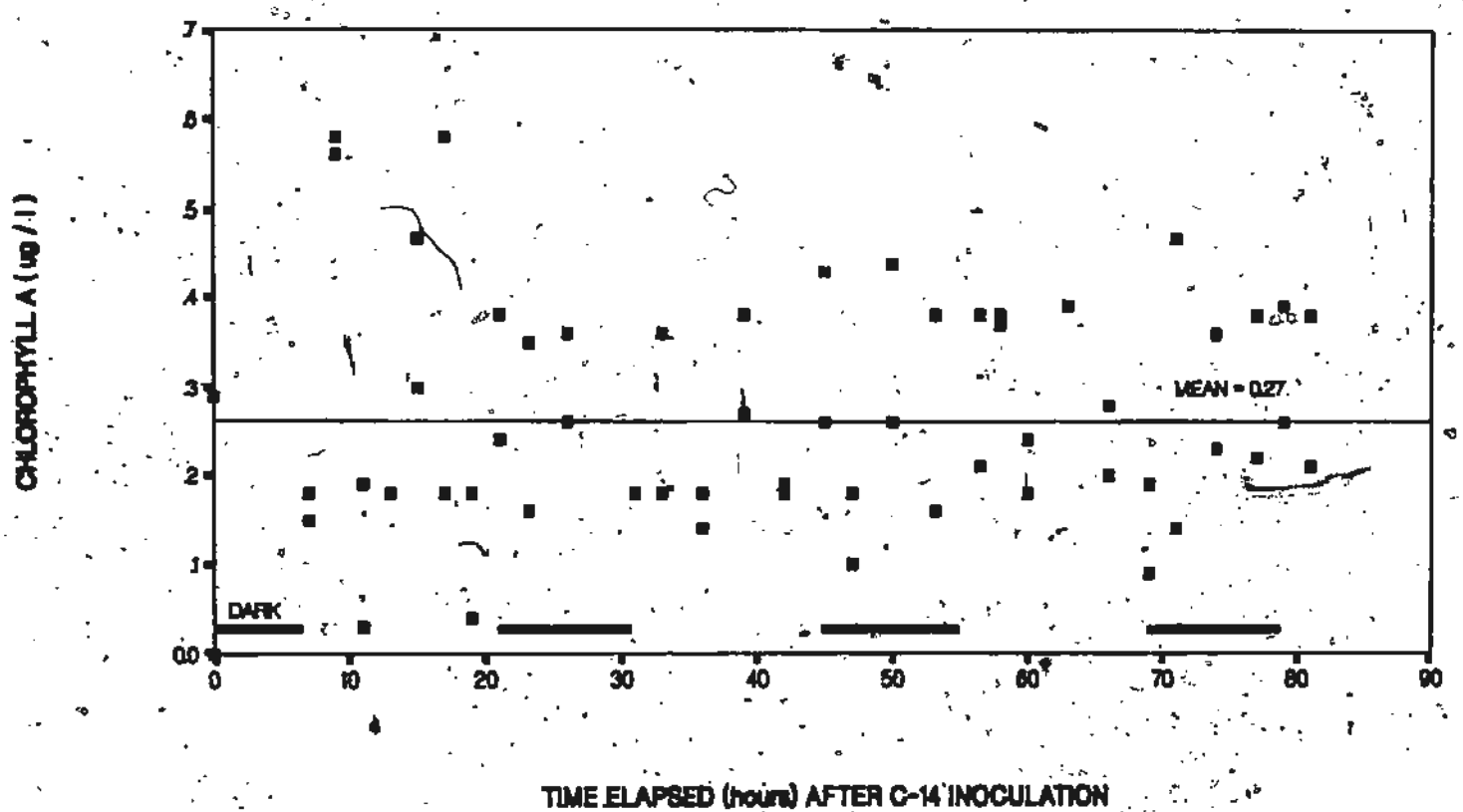
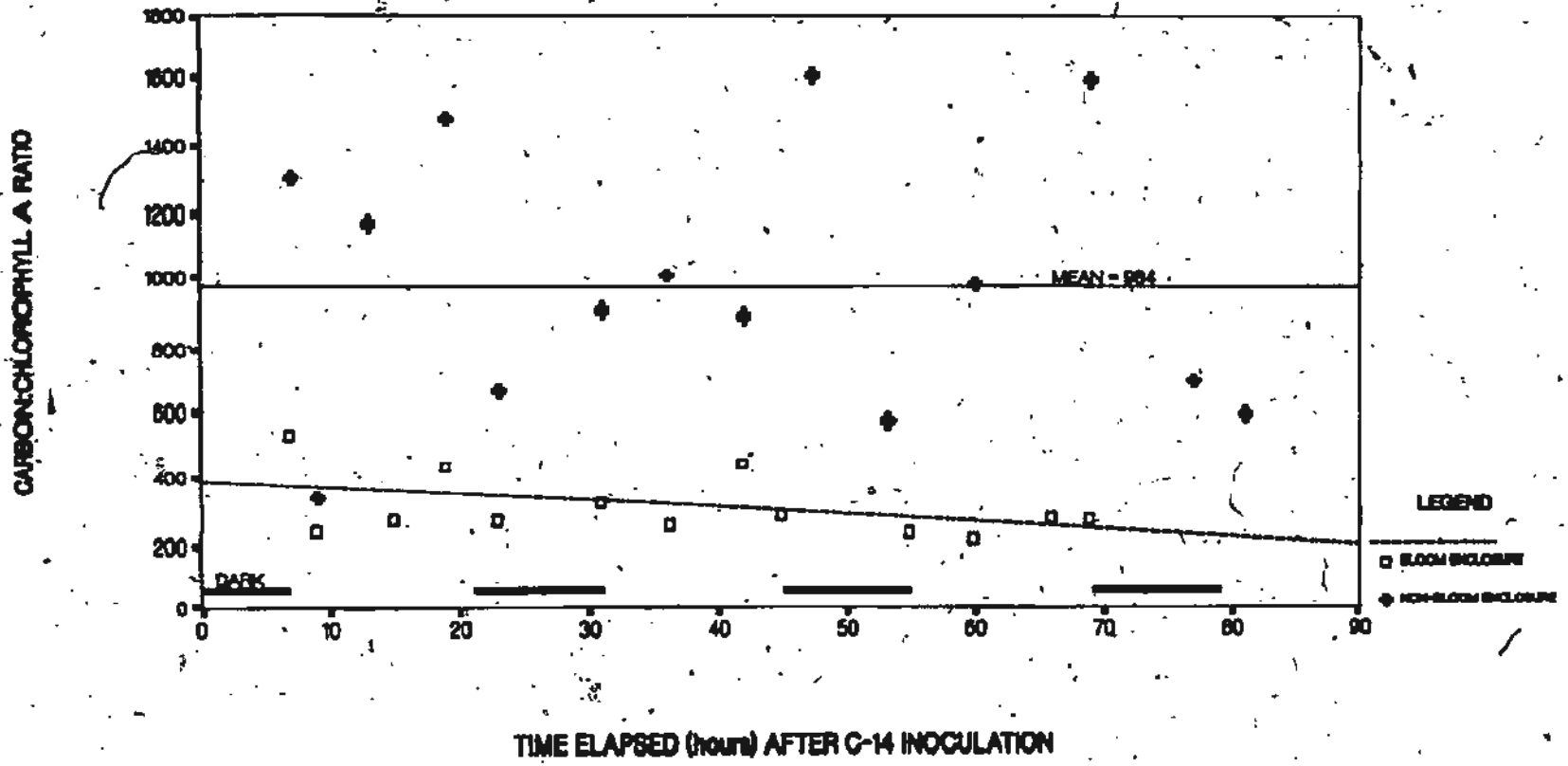


Figure 3-4: Carbon: chlorophyll *a* ratios over time in bloom and non-bloom enclosures. Significant decrease in bloom enclosure over time is shown by regression line (C:Chl *a* = 385.57 - 2.13 (time); r^2 = .21); horizontal line denotes mean ratios in the non-bloom enclosure.

PLOT OF C:CHL a RATIOS IN BLOOM AND NON-BLOOM ENCLOSURES WITH TIME



bloom POC and 22% of the non-bloom POC was composed of living phytoplankton, while the minimum estimates, using a ratio of 50, were 22% and 7% respectfully. Geiskes *et al.* 1979 observed that increases in the C:Chl *a* ratios during the course of container incubations indicated cell mortality that could be interpreted as a deleterious containment artifact. The absence of significant increases in C:Chl *a* values over time in the non-bloom enclosure (one tailed test, $p = 0.39$) and the significant decrease in the bloom enclosure (one tailed test, $p = 0.05$) can be interpreted as further evidence for the lack of containment effects (Welschmeyer and Lorenzen 1984). The decrease in bloom C:Chl *a* ratios over time does not necessarily mean that the system is becoming less stressed. The increase in resting spore abundance over time suggests this is not the case.

The bloom phytoplankton seston was dominated by *Chaetoceros spp.*, which comprised 78% of the algal biomass, with nanoplankters such as chlorophytes and cryptomonads also present. *Chaetoceros spp.* resting spores were present initially and increased in abundance during the experiment. High water temperatures ($>8^{\circ}C$) and nitrogen deficiency are both known to initiate spore production (French and Hargraves 1980); the low water temperature ($6^{\circ}C$) in the bloom enclosure leaves nutrient limitation as the likely cause for spore production, suggesting that the experiment was conducted near the end of the spring bloom. This suggestion was reinforced by low nutrient concentrations measured near the site in Bonne Bay (nitrate 0.0 to 5.7 $\mu g\ l^{-1}$, unpublished data). The non-bloom enclosure phytoplankton community was composed of chlorophyte and cryptomonad nanoplankters and lacked the diatom species commonly found in bloom conditions, suggesting that an extended period of nutrient limitation had preceded the experiment.

3.2. PRIMARY PRODUCTION

The magnitude of radiocarbon incorporation was similar for the initial day of incubation in both the bloom and non-bloom experiments. Labelled particulate carbon continued to accumulate in the bloom enclosure at an increasing rate over the three day incubation as shown by continual increases in net daily

Table 3-1: Accumulations and losses of labelled particulate carbon ($\mu g\ l^{-1}\ d^{-1}$) during bloom and non-bloom incubations.

	NET DAYTIME ACCUMULATION (dawn to dusk)	LOSS AT NIGHT (dusk to dawn)	NET DAILY ACCUMULATION (dusk to dusk)
Bloom experiment			
DAY 1	46.34	13.51	46.34*
DAY 2	98.14	19.40	84.63
DAY 3	126.24		106.84
Non-bloom experiment			
DAY 1	40.47	15.03	40.47*
DAY 2	26.37	24.85	11.34
DAY 3	33.53	19.38	8.68

* Dusk at day 0 assumed to be zero.

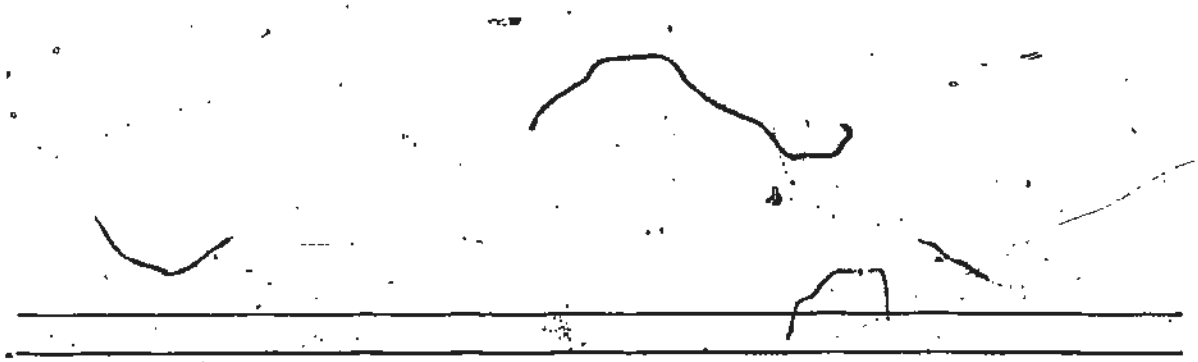
accumulations (dusk to dusk) over the 3 day incubation (Table 3-1). The rate of label accumulation in the non-bloom enclosure was observed to decrease over the 3 day experiment as shown by the decreasing net daily accumulations (dusk to dusk) of radiotracer (Table 3-1). There was a final accumulation of 238 $\mu g\ l^{-1}$ of labelled particulate carbon in the bloom enclosure as compared to only 61 $\mu g\ l^{-1}$ by the end of the non-bloom experiment. The labelled material present after 3 days constituted 76% and 32% of the total sestonic carbon (see POC measurements above) in the bloom and non-bloom enclosures respectively. These percentages can be compared to the maximum percentage of phytoplankton carbon estimates of 65% and 22% calculated above from Chl *a* levels.

In the bloom enclosure, 46 $\mu g\ C\ l^{-1}$ was accumulated by the end of day 1, 131 by day 2 and 238 by the end of day 3. The last two days of incubation demonstrated a mean net daytime accumulation (dawn to dusk) of about 112 $\mu g\ C\ l^{-1}\ d^{-1}$, over twice that observed on the first day (Table 3-1). The sky was cloudless on day 1, followed by two days of cloud cover, suggesting that lower carbon uptake on the first day might be due to photoinhibition. The enclosure was less than 1 m below the water surface and so would not have been shaded by other particulates in the water column. In contrast, net daytime radiocarbon accumulation was 40 $\mu g\ l^{-1}$ on the first day in the non-bloom enclosure and decreased on the second and third days (Table 3-1). The enclosure was again moored less than 1 m below the sea surface; however, sky conditions were uniformly sunny for the entire incubation period.

The net daytime accumulations of 98 and 126 $\mu g\ C\ l^{-1}\ h^{-1}$ on day 2 and 3 in the bloom enclosure, are greater than the maximum values recorded for the highly productive Grand Banks (*ca.* 82 $\mu g\ C\ l^{-1}\ d^{-1}$, Hollibaugh and Booth 1981, Table 3-2). Production estimates from day 1 in both bloom and non-bloom experiments (46 and 40 $\mu g\ C\ l^{-1}\ d^{-1}$) fit into the range of estimates recorded for the Grand Banks area (Table 3-2).

The net daytime accumulations of carbon during day 1 in the bloom and non-bloom enclosures (*ca.* 3.3 and 2.9 $\mu g\ C\ l^{-1}\ h^{-1}$ respectively) agree fairly well with primary production estimates of 3.0 to 5.6 $\mu g\ l^{-1}\ h^{-1}$ made in Norway by

Table 3-2: Primary production estimates for various regions of the Grand Banks in $\mu g\ C\ l^{-1}\ d^{-1}$ calculated from 0-50 m integrated production estimates ($mg\ C\ m^{-2}\ d^{-1}$) found in Hollibaugh and Booth (1981) where n= the number of estimates made and minimum and maximum describe the range of these estimates.



Region	n	Mean	Range
Northern Grand Banks	18	6.68	0.82 - 29.34
Near shore	11	15.96	1.68 - 73.70
Central Grand Banks	29	8.01	0.82 - 53.84
Shelf break region	54	11.39	0.98 - 81.80

Sargent *et al.* (1985) under similar conditions (*i.e.* large *in situ* enclosures, low temperature, natural phytoplankton populations, and low Chl *a* concentrations). Bloom production estimates on days 2 and 3 (7.0 and 9.0 $\mu g\ C\ l^{-1}\ h^{-1}$) were more than twice that observed on the first day of incubation, while the later estimates in the non-bloom enclosure (1.9 and 2.4 $\mu g\ C\ l^{-1}\ h^{-1}$ respectively) were similar to those on the initial day of incubation.

There were decreases in labelled POC during the dark periods in both experiments. The diatom-dominated bloom enclosure lost an average of 24% of the net daytime accumulation of radiotracer overnight while 63% was lost overnight in the nanoplankton-dominated (chlorophytes and cryptomonads) non-bloom enclosure (Table 3-1). Loss of POC may represent respiration of organic matter into DIC or production of dissolved organic carbon (DOC) through either leakage, secretion or cell damage due to grazing. The production of DOC can be examined by comparing the level of TOC produced with that of the POC products. Such comparisons have not routinely been done in oceanic studies; however, Pissierssens *et al.* (1985) have recently argued for their importance. The fact that the $TO^{14}C$ values corresponded very closely to those for $PO^{14}C$ in the current experiments (Figures 3-5 and 3-6) indicates that overnight decreases in $PO^{14}C$ activity were likely due to respiration and not the production of DOC. There appears to have been some production of DOC during the last daylight period in the bloom enclosure and the last night time period in the non-bloom enclosure. Overall, however, DOC production must have been low or else any DOC produced must have been rapidly converted into POC by microbial activity.

The net daily accumulation of radiotracer in the bloom POC increased in magnitude each day over the 3 day incubation while the non-bloom net daily accumulation decreased over time (Table 3-1) suggesting the system was saturating with radiotracer; *i.e.* the flux of label into the POC pool approached the flux out (net daily accumulation approached 0). The calculation of the flux of carbon into the POC pool then becomes more complicated because the observed flux must be corrected for the secondary and back reaction fluxes.

Figure 3-5: Concentration of total organic ^{14}C and particulate organic ^{14}C over time in bloom enclosure with standard errors denoted by vertical bars.

CONCENTRATION OF TOTAL ORGANIC C-14 AND PARTICULATE ORGANIC C-14 OVER TIME IN BLOOM ENCLOSURE

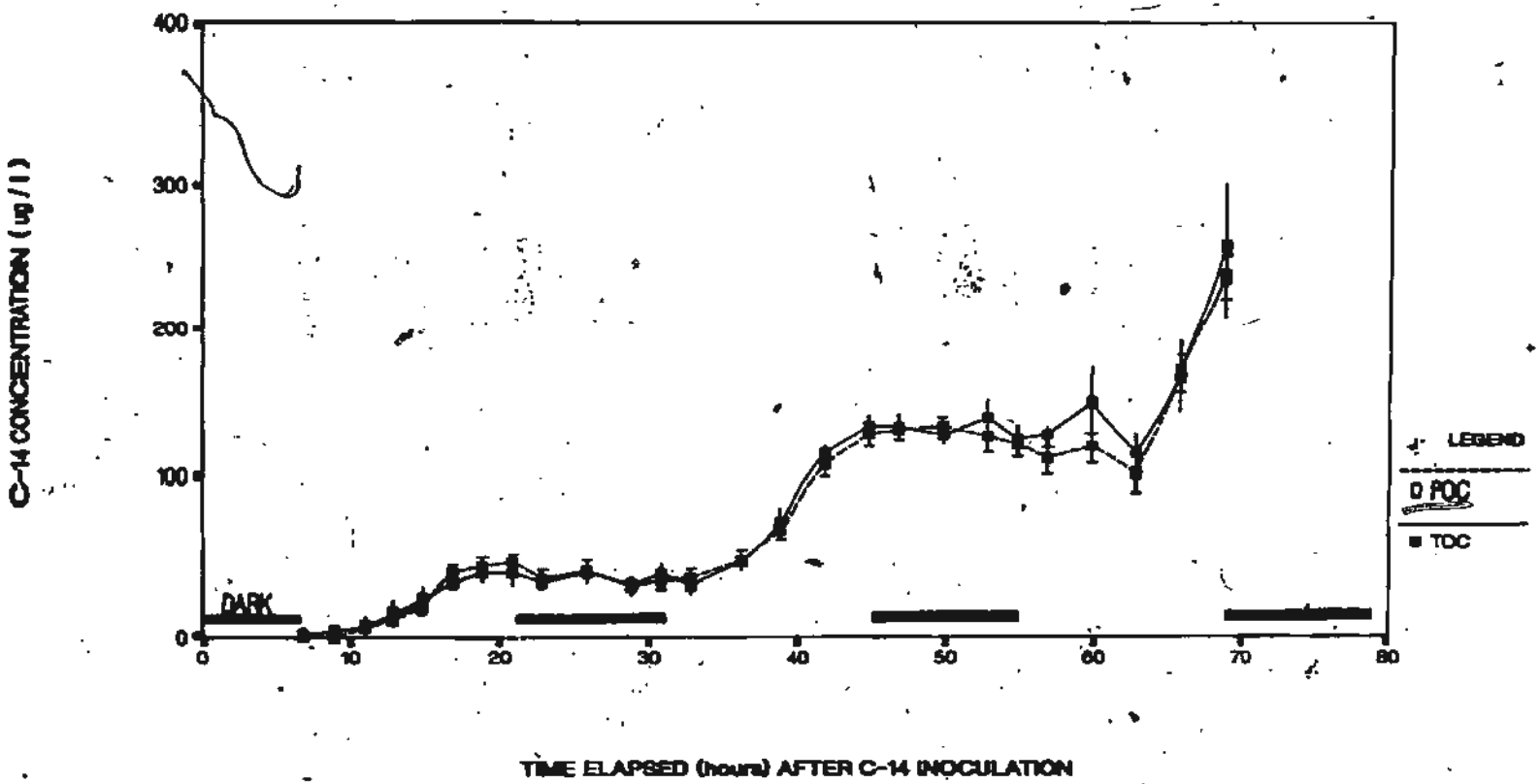
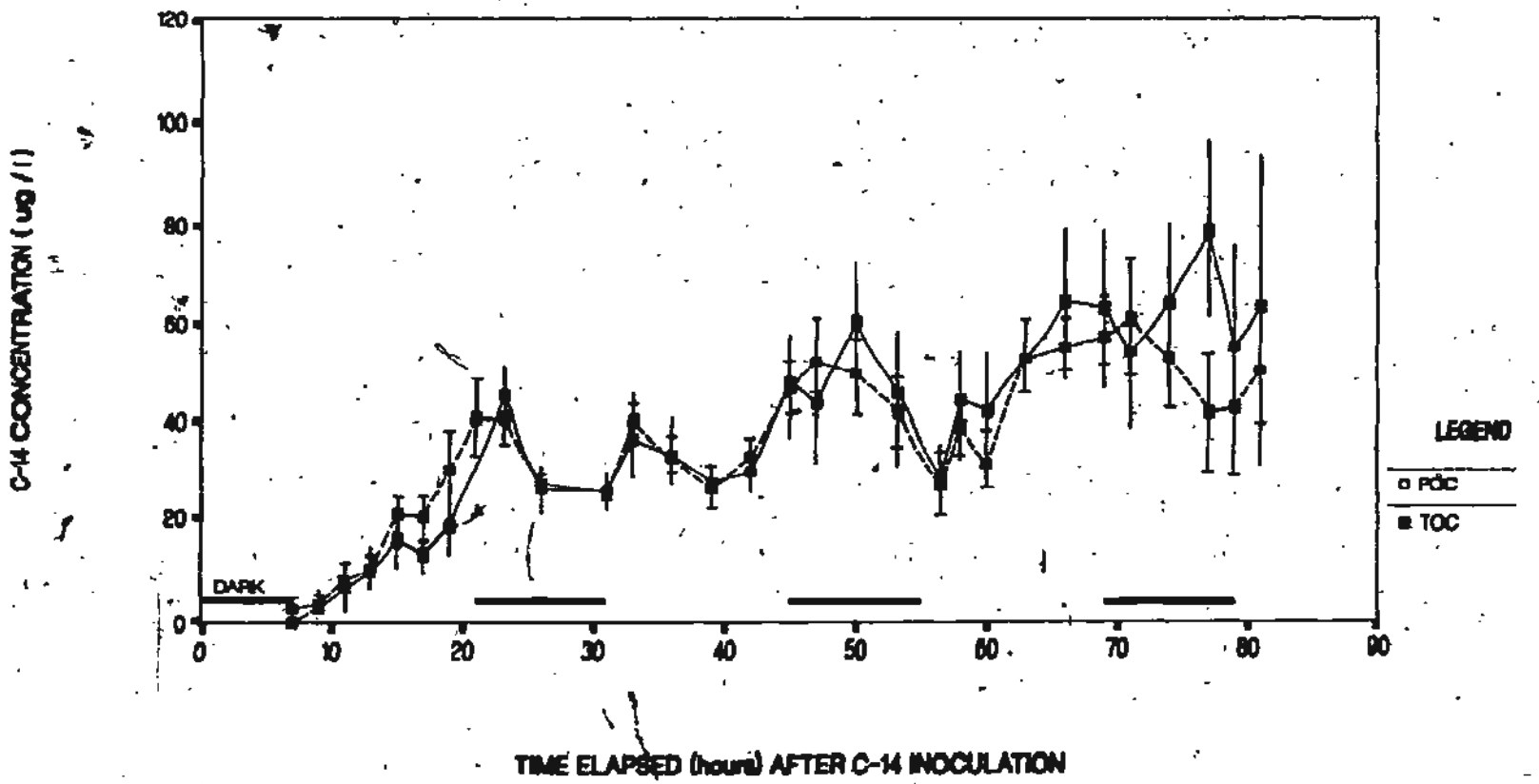


Figure 3-6: Concentration of total organic ^{14}C and particulate organic ^{14}C over time in non-bloom enclosure with standard errors denoted by vertical bars.

CONCENTRATION OF TOTAL ORGANIC/C-14 AND PARTICULATE ORGANIC C-14 OVER TIME IN NON-BLOOM ENCLOSURE



3.2.1. SATURATION EFFECTS

It is usually assumed in C^{14} production experiments that the specific activity of the product pool remains so low relative to that of the substrate pool that back or secondary reactions do not substantially affect the amount of label accumulated in the product pool. In situations where the product pool does approach saturation with tracer, the net daily accumulation of tracer should approach zero as flux rates of tracer into and out of the pool approach equality. The accumulation of $PO^{14}C$ in the bloom enclosure was approaching the total sestonic POC level while the net daily accumulation approached zero in the non-bloom enclosure, suggesting that both experiments might be saturating.

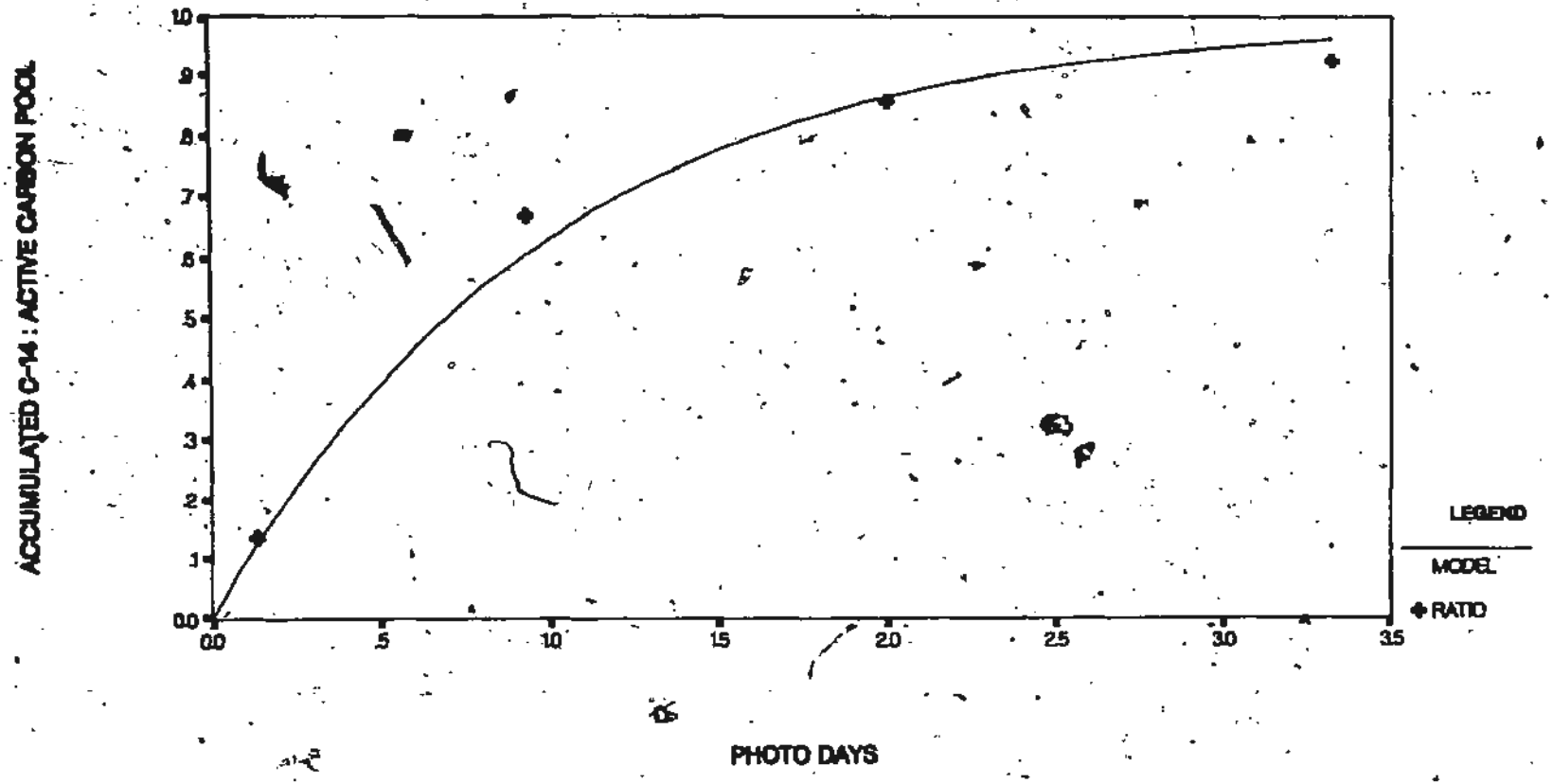
If a large proportion of the POC pool is labelled during the experiment, then the amount of isotope accumulated in the pool may be an underestimate of the true flux rate because back reactions are of a sufficient magnitude to mask the flux of radiotracer into the pool. A corrected estimate of carbon flux can still be made if saturation kinetics are taken into account.

In order to decide whether or not the carbon uptake data should be interpreted using a saturation model (see methods, p. 20) it is necessary to determine if saturation has taken place. The pattern of ^{14}C labelling can be compared to that predicted from saturation kinetics based on the observed pool size and turnover times (*i.e.* the time it takes the active carbon pool to become half-labelled: Welschmeyer and Lorenzen 1984). This is best illustrated if only the peak measurements of daily carbon fixation are used in the equation so that the diurnal fluctuations of carbon that often occur are left out (Rivkin 1985).

If the specific activity of the product pool (the ratio of accumulated radiotracer to the maximum size of the product pool) is plotted against time, and saturation is occurring, then the ratio determined from experimental values will lie along the saturation curve (Welschmeyer and Lorenzen 1984). The saturation curve provides a very good fit to the observed pattern of $PO^{14}C$ accumulation in the non-bloom experiment (Figure 3-7). The poor fit of the points to the saturation curve suggests that back reactions were not yet a problem in the bloom enclosure (Figure 3-8) despite the fact that the $PO^{14}C$ accumulation in the bloom

Figure 3-7: Curve predicted from saturation model for ^{14}C uptake by live portion of non-bloom seston over time (in photodays, where one photoday is the daylight portion of the day). The points fit the curve very well, indicating that the saturation model is appropriate to describe the ^{14}C uptake in this case.

SATURATION MODEL FOR C-14 INCORPORATION OVER TIME BY LIVE PORTION OF NON-BLOOM SESTON



experiment approached the magnitude of the total sestonic POC pool by the third day. This could be explained if the living POC pool was expanding in size. The measurable increase in Chl *a* concentration over time in the bloom enclosure strongly suggests that there was an expansion of the phytoplankton portion of the POC pool even though the total amount of seston POC did not significantly change. Overall, the results indicate that it is appropriate to correct the flux measurements for the non-bloom enclosure and not for the bloom enclosure.

A corrected flux can be calculated for a time period prior to complete saturation using an equation similar to that used by Conover and Francis (1973) for the correction of isotope fluxes between trophic levels:

$$\text{Corrected flux} = \textit{observed flux} \times \left[1 - \frac{\textit{observed flux}}{\textit{total pool size}}\right]^{-1}$$

where the corrected flux is the total carbon incorporation up to time x, the observed flux is the amount of carbon accumulation observed at time x, and the total pool size is estimated as the level of $PO^{14}C$ observed at saturation (the metabolically active carbon pool size).

The corrected daytime flux calculated for day 1 in the non-bloom enclosure is 120 μg C l^{-1} d^{-1} (ca. 8.6 μg C l^{-1} h^{-1}), similar to the maximum rate of 126 μg C l^{-1} d^{-1} observed in the bloom enclosure, where Chl *a* levels were twice as high (Table 3-1). Thus the two experiments differed little in gross primary production while markedly differing in the disposition of that production.

3.3. SPECIES SPECIFIC CARBON FLOW

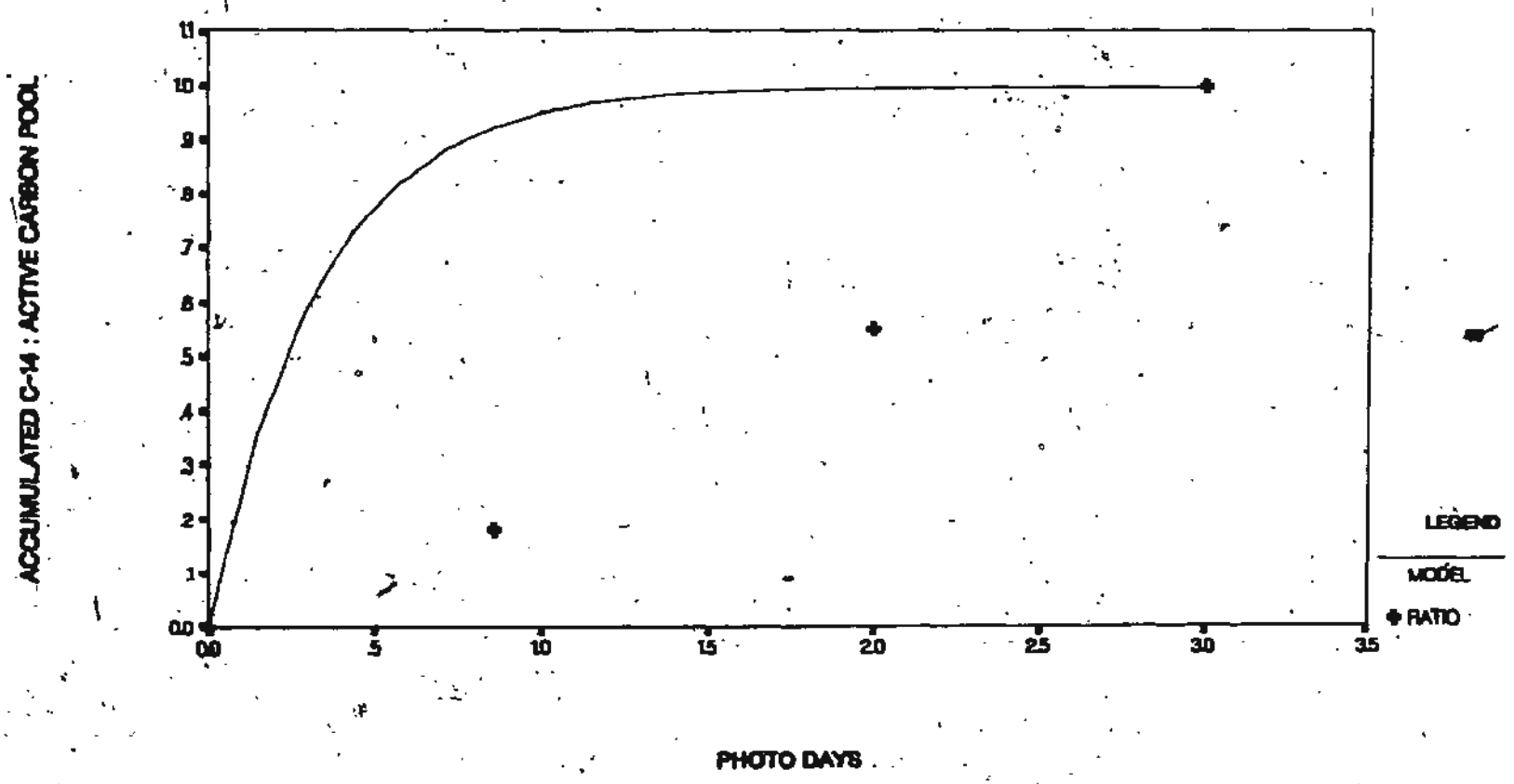
3.3.1. CELL ABUNDANCE AND DIVISION

Changes in cell abundance over time can be used to estimate net population growth rates and can also serve as a parameter in the calculation of specific carbon contributions to the POC over time.

Overall cell abundances, including both micro and nanoplankton, were observed to increase throughout the incubation in the bloom enclosure (Table 3-3)

Figure 3-8: Curve predicted from saturation model for ^{14}C uptake by live portion of bloom seston over time (in photdays, *i.e.* time based only on the daylight portion of the day). The poor fit of points to curve suggests that saturation kinetics are inappropriate for this experiment.

SATURATION MODEL FOR C-14 INCORPORATION OVER TIME BY LIVE PORTION OF BLOOM SESTON



while total cell abundance in the non-bloom enclosure increased only on day 3 (Table 3-4).

A 62% increase in abundance was observed in the bloom microplankton (diatoms, largely *Chaetoceros spp.*) during the second day of incubation while a 60% increase occurred in the nanoplankton component (Table 3-3), due chiefly to chlorophyte increase on the third day. In comparison, the chlorophytes increased by 33% on the third day of the non-bloom experiment (Table 3-4), while cryptomonads remained at low levels throughout in both enclosures.

3.3.2. CELLULAR CARBON FLOW

The use of ^{14}C track autoradiography allowed the estimation of carbon content and carbon uptake rates for individual taxa. Culture work suggests that rapidly growing algal cells are between 10% and 15% carbon on a weight : volume (w/v) basis (Mullin *et al.* 1966; Healey 1975). Ratios in non-growing cells may either be higher, as French and Hargraves (1980) have shown in the case of some diatom resting spores, or perhaps lower, as proposed by Caperon and Meyer (1972) for cells intolerent to nutrient stress.

The mean proportion of the chlorophyte and cryptomonad cellular biomass (w/v) labelled by the end of the bloom incubation was approximately 10.3%, less than expected for cells in logarithmic growth (Cushing *et al.* 1958b, 12%; Mullin *et al.* 1966, 15%), while only 4.1% of cell volume was labelled carbon in the non-bloom enclosure.

The nanoplankton chlorophytes and cryptomonads accumulated much less carbon on a weight : volume basis in the non-bloom enclosure compared to the bloom enclosure. Chlorophytes in the bloom enclosure achieved 3.7% (w/v) carbon on the first day and then continued to accumulate more label each day, reaching a level of 7.6% (w/v) by the end of the experiment (Figure 3-9). Similar taxa in the non-bloom enclosure reached 4.4% on the first day, not significantly different from the bloom enclosure, but then failed to reach higher levels throughout the remainder of the experiment (Figure 3-9). The carbon contents of the cryptomonads also were not significantly different between enclosures at the

Table 3-3: Cell abundance (cells ml^{-1}) for various taxa over time for bloom enclosure with standard errors for estimates calculated assuming a Poisson distrubution.

TAXONOMIC GROUP	DAY 1 (16.8 h)*	DAY 2 (41.8 h)	DAY 3 (65.8 h)
	VEGETATIVE CELLS		
DIATOMS			
Chaetoceros spp.	864 ±51	1307 ±63	1306 ±63
Nitzschia seriata	7 ± 3	11 ± 4	9 ± 4
Thallassiosira spp.	15 ± 7	30 ±10	24 ± 8
NANOPLANKTON			
chlorophyta	982 ±58	997 ±55	1587 ±70
cryptophyta	43 ±11	21 ± 8	44 ±11
	RESTING SPORES		
C. diadema	15 ± 5	21 ± 8	13 ± 6
C. spp.	35 ±12	124 ±19	195 ±24
GRAND TOTAL	1961 ±147	2511 ±167	3178 ±186

* Time elapsed since beginning of experiment

Table 3-4: Cell abundance (cells ml^{-1}) for various taxa over time for non-bloom enclosure with accompanying standard errors for counts calculated assuming Poisson distribution.

TAXONOMIC GROUP	DAY 1 (21.0 h)*	DAY 2 (45.0 h)	DAY 3 (66.0 h)
chlorophyta	1958 ±77	1888 ±68	2553 ±88
cryptophyta	21 ± 8	20 ± 8	26 ± 9
GRAND TOTAL	1979 ±85	1909 ±76	2579 ±97

* Time elapsed since beginning of experiment

Figure 3-9: Carbon incorporation over time for chlorophytes in bloom and non-bloom enclosures showing standard error of estimates.

CARBON INCORPORATION OVER TIME FOR CHLOROPHYTES IN BLOOM AND NON-BLOOM ENCLOSURES

BASED ON C-14 TRACK AUTORADIOGRAPHY

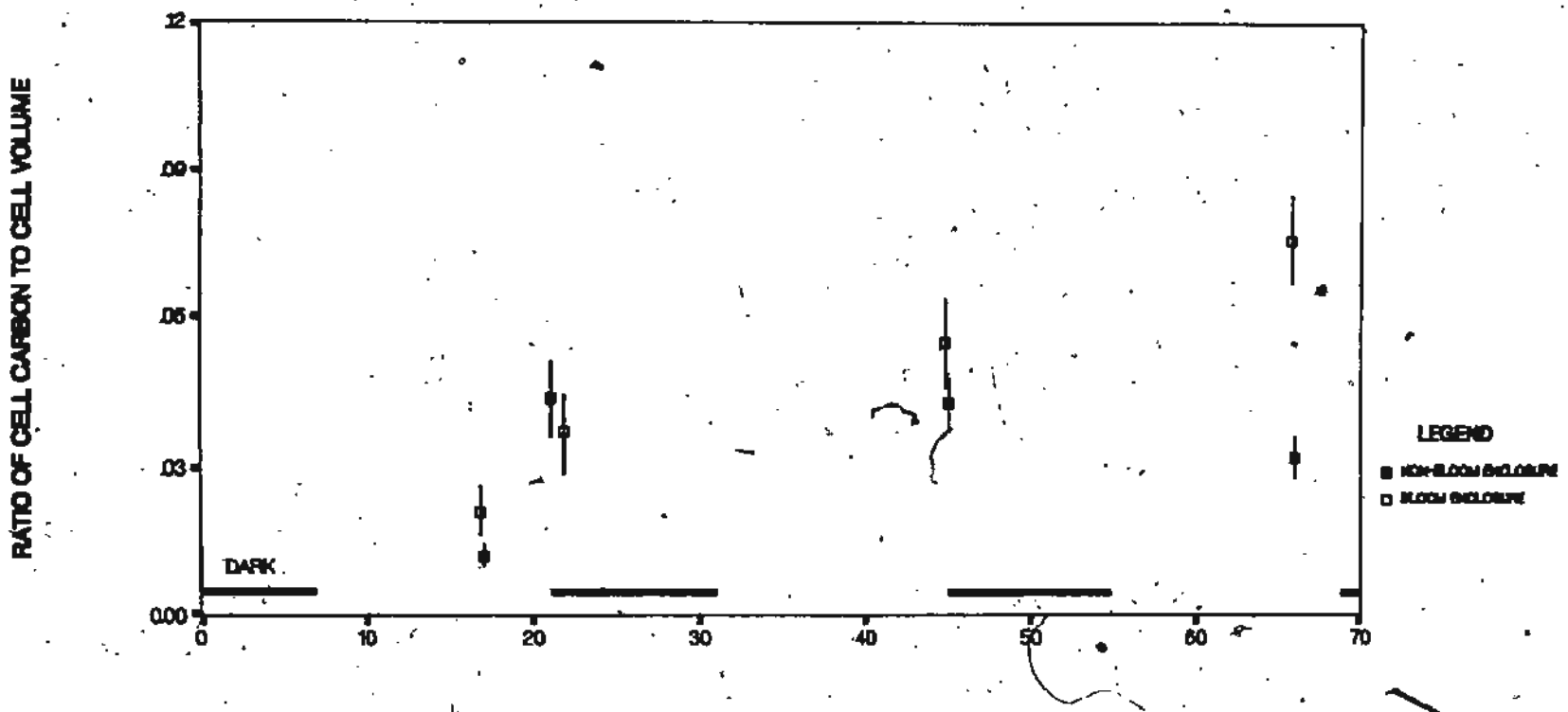
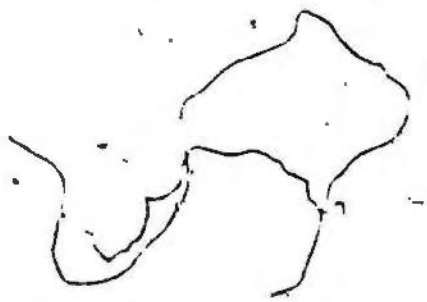
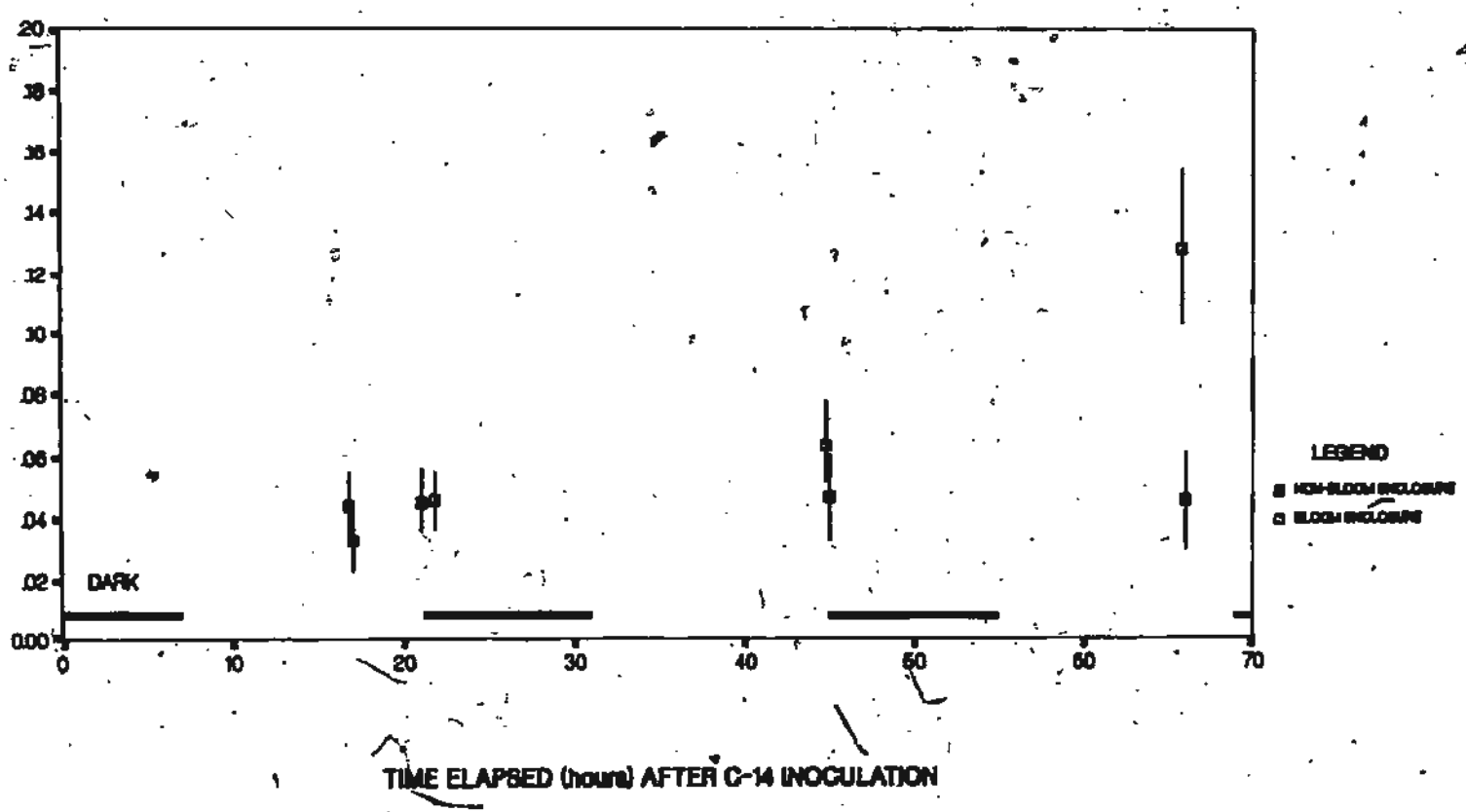


Figure 3-10: Carbon incorporation over time for cryptomonads in bloom and non-bloom enclosures showing standard error of estimates.



CARBON INCORPORATION OVER TIME FOR CRYPTOMONADS IN BLOOM AND NON-BLOOM ENCLOSURES

BASED ON C-14 TRACK AUTORADIOGRAPHY



end of the first day (Figure 3-10), with levels of 4.6% and 4.5% carbon respectively, but levels again remained static in the non-bloom enclosure whereas the bloom cryptomonads reached 12.9%. The data thus indicate that the non-bloom cells were turning over smaller carbon pools, and given that similar absolute amounts of carbon were taken up the first day in both experiments, the smaller pools were therefore turning over more rapidly. It cannot be determined if the total cellular carbon pool is actually smaller during non-bloom conditions or if perhaps only part of the pool is being labelled (metabolically active). If the latter is the case, it would imply that the cells were not actually dividing but instead just replacing a portion of their carbon each day.

The diatom *Chaetoceros spp.* was found only in the bloom enclosure and accumulated carbon amounting to 10.4% of it's cell biomass (Figure 3-11). This track autoradiography-based estimate of cell carbon agreed very well with an independent estimate of approximately 13.2% for the genus *Chaetoceras* grown in culture (Strathman 1967).

Approximately 11% of the vegetative *Chaetoceros spp.* cell biomass (the bulk of which was assumed to be *C. diadema* due to cell size) was labelled by the end of the 3 day bloom incubation (Figure 3-11), compared to 48% for *C. diadema* resting spores (Table 3-5). French and Hargraves (1980), working with laboratory cultures, observed that resting spores of the genus *C. diadema* had up to 4.4 times that cellular carbon content when compared to the vegetative cells of the same species; in the current study, there was a 4.3 fold difference between large vegetative *C. spp.* (probably *C. diadema*) and the resting spores of *C. diadema* (Table 3-5). The carbon content of other *C. spp.* resting spores was difficult to compare as fewer corresponding vegetative cells were present in the samples.

The incorporation of new carbon by *N. seriata* was monitored in more detail than that of *Chaetoceros spp.* due to ease of counting and identification. Generally, cellular radiocarbon increased during the daylight hours but irregular fluctuations in cell radiocarbon content were observed and there was also an increase in cell carbon during the second night (Figure 3-12); fluctuations have

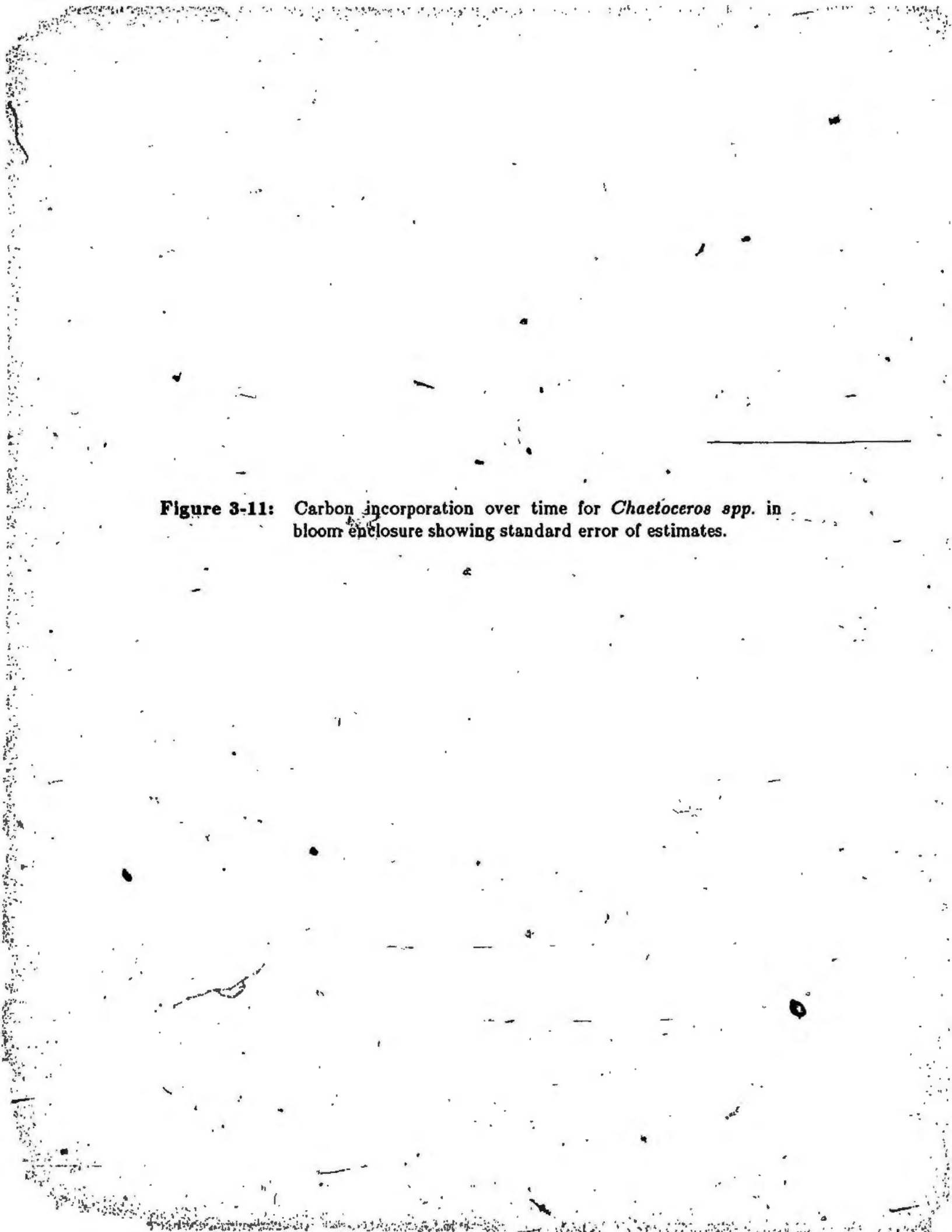


Figure 3-11: Carbon incorporation over time for *Chaetoceros spp.* in bloom enclosure showing standard error of estimates.

CARBON INCORPORATION OVER TIME FOR CHAETOCEROS SPP. IN BLOOM ENCLOSURE

BASED ON C-14 TRACK AUTORADIOGRAPHY

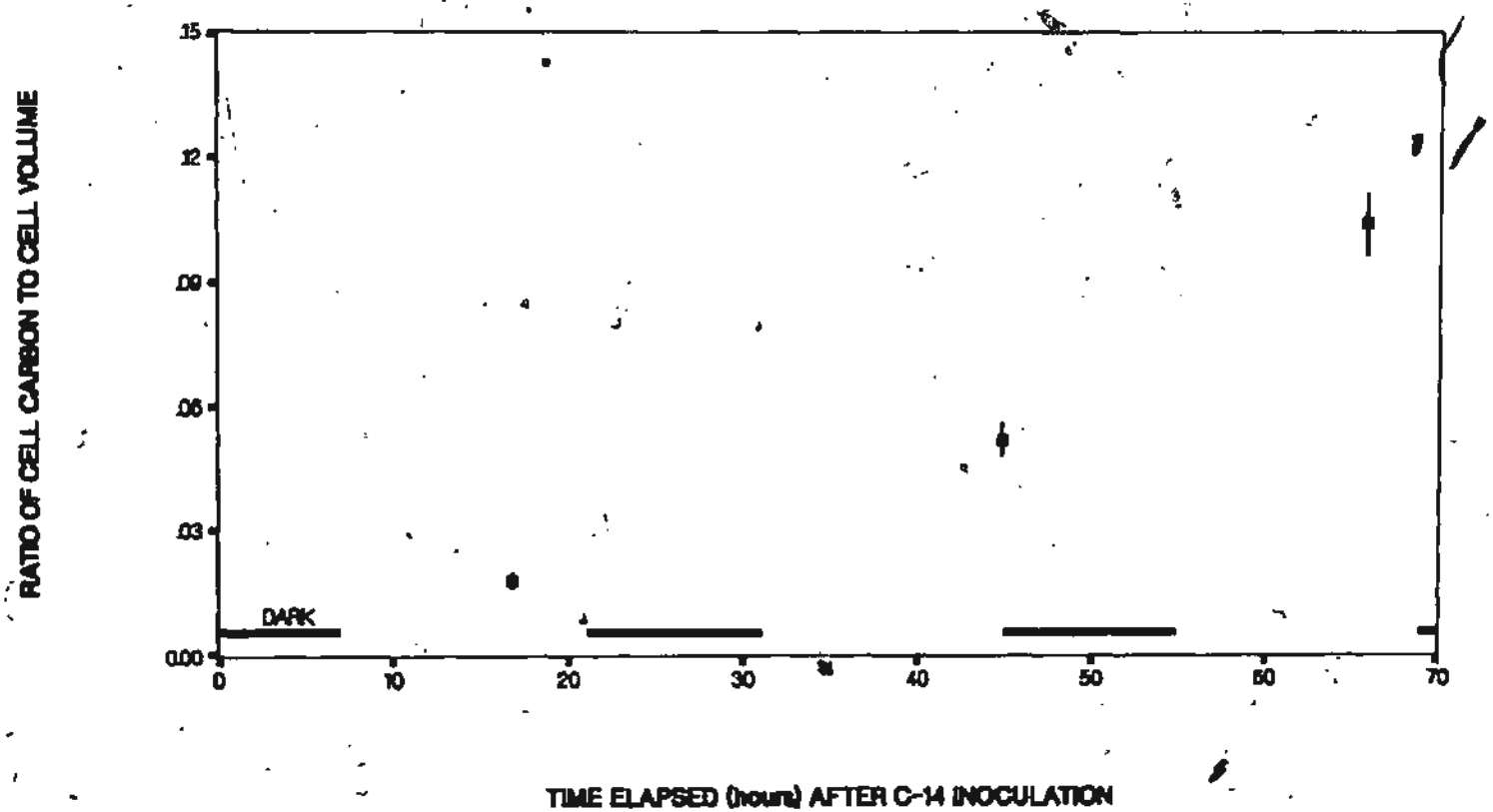
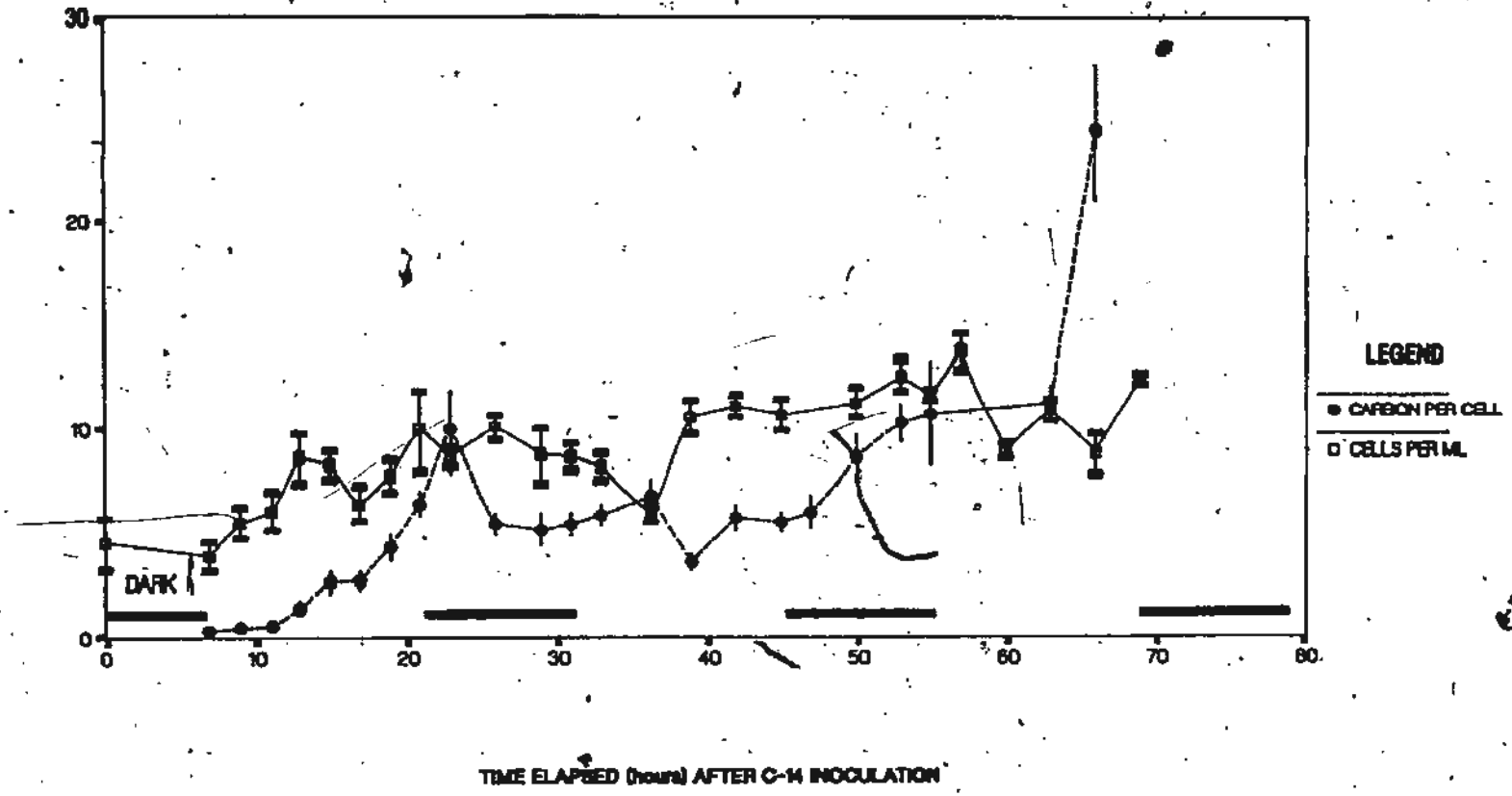


Table 3-5: Incorporation of new carbon, as a ratio of cell volume, over time for vegetative cells and resting spores of *Chaetoceros spp.* in bloom enclosure.

TAXONOMIC GROUP	DAY 1 16.8 h	DAY 2 41.8 h	DAY 3 65.8 h
Resting spores			
C. diadema	9.35	20.68	48.14
Chaetoceros spp.	2.82	4.58	10.51
Vegetative cells			
Chaetoceros spp.	3.30	3.88	11.31

Figure 3-12: Cell abundance and carbon incorporation over time of the diatom *Nitzschia seriata* for bloom enclosure.

CELL ABUNDANCES AND AUTORADIOGRAPHY ESTIMATES OF CARBON CONTENT FOR THE DIATOM Nitzschia seriata OVER TIME IN BLOOM ENCLOSURE



also been reported on the population level for monocultures of other marine phytoplankters (Barlow 1984a, Rivkin 1985). *N. seriata* cells accumulated 10.0 pg C by the end of day 1 and did not increase again until day 3 (Appendix D). Sharp drops in carbon content per cell were observed twice during the incubation (Figure 3-12), once in early evening (at 24 h) and once in mid day (at 39 h). Declines in cell carbon could be due to loss of label through respiration, excretion and secretion or to a reduction in cell volume resulting from cell division. Cell abundance estimates indicate a synchronous cell division occurred prior to the 39 h sampling point corresponding to the observed 50% decrease in C cell^{-1} from 6.9 pg to 3.4 pg (Figure 3-12). The sharp drop in cell carbon between 23 h and 31 h (Figure 3-12) was not accompanied by a measurable increase in abundance and thus must represent either very rapid respiration, secretion; excretion processes or a shift in susceptibility of the label to loss on preservation (see below).

Radiocarbon per cell was observed to increase unexpectedly during the second night of incubation. There is no known pathway for major carbon incorporation at night in diatoms. It is possible that photosynthate was already present in the cell at dusk but in a form that was more susceptible to leaching by the preservative. Cuhel *et al.* (1984) have shown that carbon accumulated in the cell during daytime in the form of storage products such as lipids or carbohydrates can be used to produce proteins during the night; proteins should be less susceptible to loss on preservation as the fixatives generally bind to them (Silver and Davoll 1978). In the current study, a decrease in loss on preservation during the night was in fact observed (see section 3.3.3 below). *N. seriata* had accumulated 24.4 pg of labelled carbon by the end of the incubation, amounting to 13.6% of its cell biomass, a percentage similar to that recorded for other diatoms (13.6% for *Chaetoceros*, Strathman 1967). The ability to measure cellular carbon pool sizes accurately during cellular cycles such as the synchronous cell division, shown in Figure 3-12, identifies the use of track autoradiography as an important method for the investigation of carbon flow at the cellular level in natural phytoplankton assemblages.

3.3.3. SPECIFIC CARBON CONTRIBUTIONS

The autoradiographic analysis of particulate matter settled onto microscope slides permits radioactivity to be attributed to specific sources. The specific carbon contributions to the $PO^{14}C$ pool can be calculated from cell abundances (cells ml^{-1}) and corresponding track autoradiographic estimates of radiocarbon per cell. The product of these components can be compared directly to the $PO^{14}C$ after correction for radiotracer loss on preservation. Silver and Davoll (1978) noted losses of filter-retainable activity following iodine preservation and variation in the loss with respect to the phytoplankton population being studied. Lugols-preserved samples were used in the preparation of track autoradiography slides; therefore, preserved samples were filtered for comparison with fresh, unpreserved filters.

Measurements of $PO^{14}C$ on filters from preserved samples were lower than the corresponding unpreserved values. The proportionate drop in activity was examined by linear regression. The regression slopes were 0.36 and 0.61 for the bloom and non-bloom experiments respectively (Figures 3-13 and Figure 3-14) indicating, that preservation losses were higher in the bloom enclosure (64%) than in the non-bloom experiment (39%; see Appendix E for data). Despite the high correlations ($r^2 = 0.95$ and $r^2 = 0.91$), there were obvious diurnal patterns in the ratio of preserved : unpreserved filter activity. There was a rapid increase in the ratio, indicating reduced susceptibility to loss during the first day of incubation in both experiments (Figure 3-15 and Figure 3-16). After the first daylight period, there were usually increases in the ratio during each night followed by declines during the day. This observation is consistent with the pattern of daytime accumulation of storage products followed by night time conversion to proteins observed by Barlow (1984b) and Cuhel *et al.* (1984).

Specific phytoplankton carbon contributions were determined by multiplying cell abundance of a taxon with the corresponding mean cellular (track autoradiography-based) radiocarbon estimate. Identifiable sources of labelled carbon ranged from 57 to 86% (mean= 72%) of the $PPO^{14}C$ in the bloom enclosure (Table 3-6), with no consistent pattern over the 3-day incubation, while

Figure 3-13: Regression of preserved with unpreserved filters for bloom enclosure (Preserved $PO^{14}C = -0.99 + 0.34$ (Unpreserved $PO^{14}C$); $r^2 = 0.95$.

REGRESSION OF PRESERVED PARTICULATE ORGANIC C-14 WITH UNPRESERVED PARTICULATE ORGANIC C-14 OVER TIME

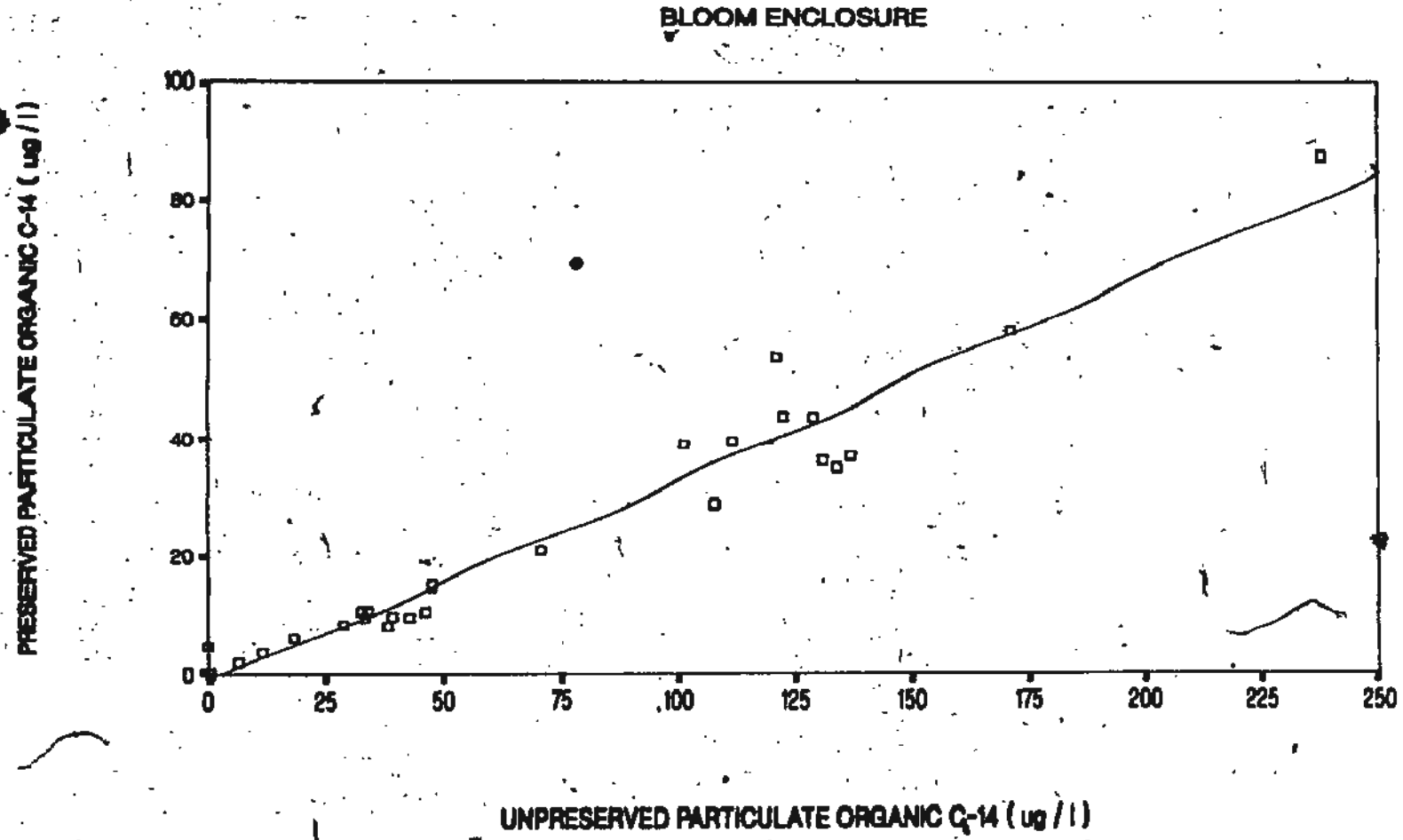


Figure 3-14: Regression of preserved with unpreserved filters for non-bloom enclosure (Preserved $PO^{14}C = -1.56 + 0.54$ (Unpreserved $PO^{14}C$); $r^2 = 0.91$).

REGRESSION OF PRESERVED PARTICULATE ORGANIC C-14 WITH UNPRESERVED PARTICULATE ORGANIC C-14 OVER TIME

NON-BLOOM ENCLOSURE

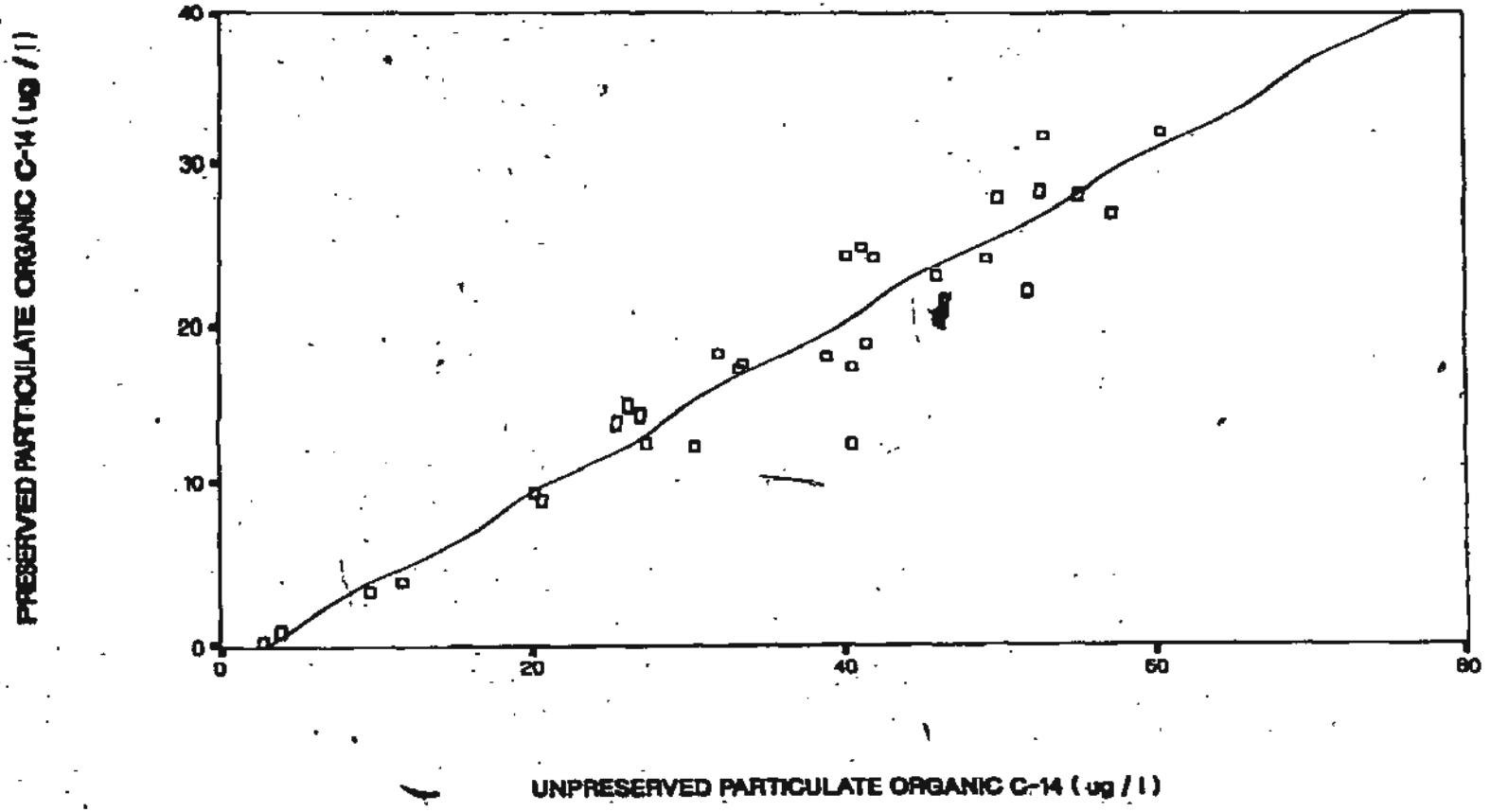


Figure 3-15: Plot of ratio of preserved : unpreserved particulate organic ^{14}C over time in bloom enclosure showing diurnal fluctuations. The ratio tends to increase during the night and decrease during the day with the exception of day 1.

RATIO OF PRESERVED PARTICULATE ORGANIC C-14 TO UNPRESERVED PARTICULATE ORGANIC C-14 OVER TIME IN BLOOM ENCLOSURE

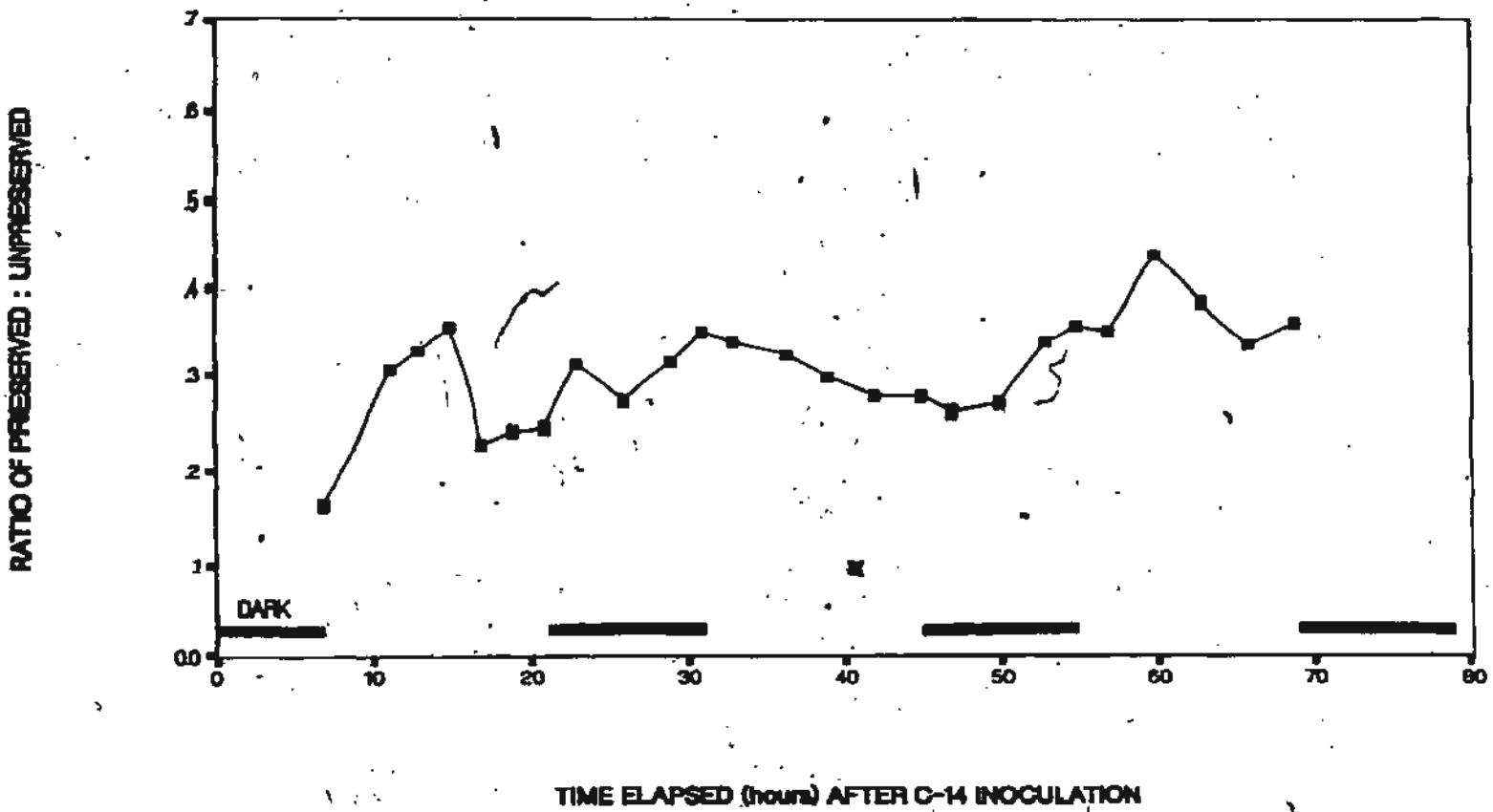
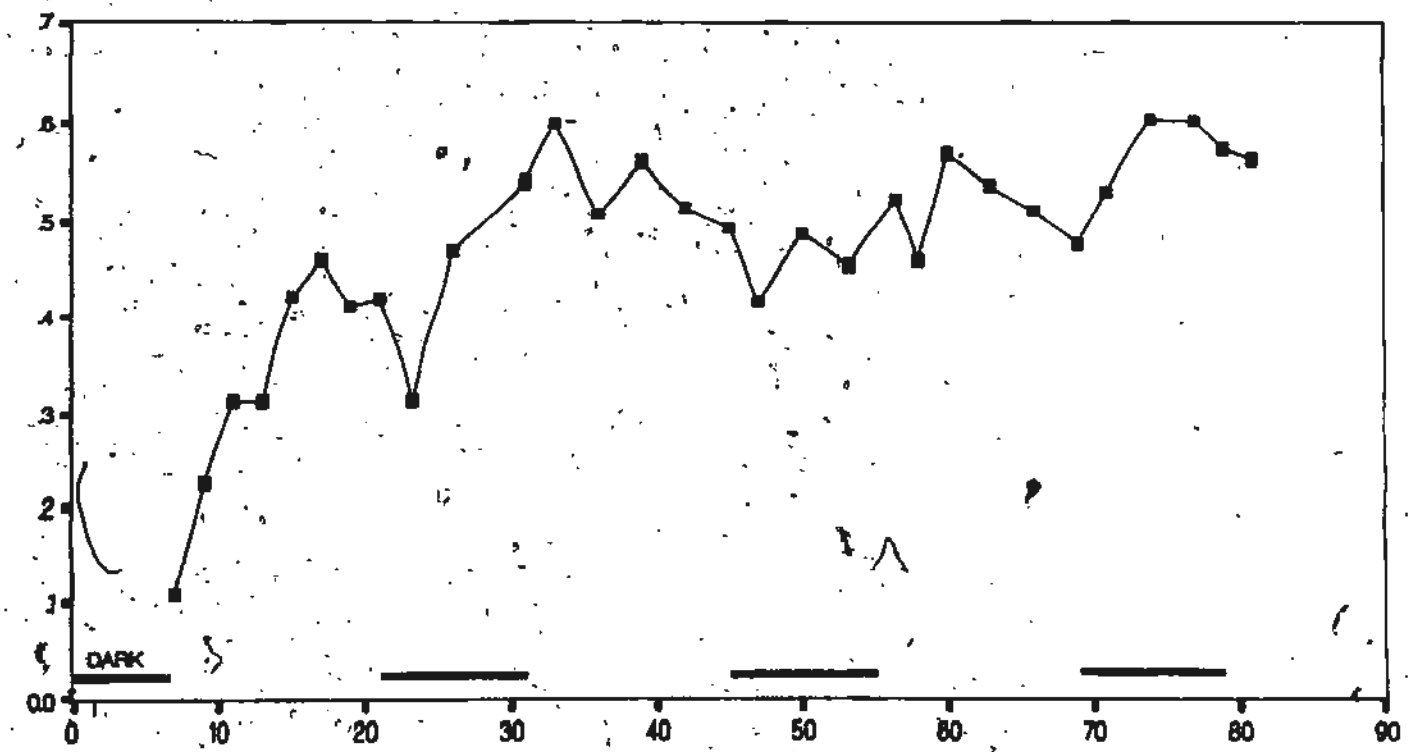


Figure 3-16: Plot of the ratio of preserved to unpreserved particulate organic ^{14}C over time for non-bloom enclosure showing increasing ratio during day 1 and subsequent nights. The following daytime periods show a decreasing trend in the ratio.

RATIO OF PRESERVED PARTICULATE ORGANIC C-14 TO UNPRESERVED PARTICULATE ORGANIC C-14 OVER TIME IN NON-BLOOM ENCLOSURE



identifiable sources declined from 30% to 20% (mean = 25%) in the non-bloom experiment (Table 3-7).

Total nanoplankton (chlorophytes plus cryptomonads) carbon levels were similar in the two experiments, accounting for 8.6 μg C l^{-1} at the end of the bloom experiment and 5.7 μg C l^{-1} at the end of the non-bloom incubation. The bulk of the particulate activity in the bloom experiment was attributable to diatoms, increasing from 45% at the end of the first day to 71% at termination, while the portion of the particulate activity in the non-bloom experiment which could be attributed to identifiable sources declined from 30% at the end of day 1 to 20% at termination.

The unidentifiable particulate radioactivity was indeed present on the autoradiography slides, as evidenced by agreement between total track counts per unit area of slide (and consequently per unit volume of water) and filter-retained preserved $PO^{14}C$ estimates. For example, non-bloom enclosure filter estimates for 21 and 45 h were 17.1 and 22.6 μg C l^{-1}, while the track per field data generated estimates of 15.3 and 23.9 μg C l^{-1} respectively: differences of -11% and +5%.

It is thus clear that the bulk of the labelled carbon in the non-bloom enclosure was associated either with living cells too small to see with the light microscope, such as bacteria, or with non-living detrital or colloidal material. It has been observed in freshwater that high molecular weight extracellular colloids can constitute as much as 60% of the 'particulate' radioactivity retained on membrane filters (Schindler *et al.* 1972).

Table 3-6: Contributions of carbon (μg C l^{-1}) by various taxa to bloom POC pool over time as estimated from ^{14}C track autoradiography and cell abundance data.

	BLOOM ENCLOSURE		
TAXONOMIC GROUP	DAY 1 (16.8 h)	DAY 2 (41.8 h)	DAY 3 (65.8 h)
	VEGETATIVE CELLS		
DIATOMS			
Chaetoceros spp.	4.12	11.11	35.47
Nitzschia seriata	0.02	0.06	0.22
Thalassiosira spp.	0.19	0.72	1.79
NANOPLANKTON			
chlorophyta	1.65	3.44	7.32
cryptophytes	0.17	0.26	1.24
	RESTING SPORES		
C. diadema	0.27	0.82	1.18
C. spp.	0.11	0.65	2.35
PHYTOPLANKTON CARBON TOTAL	6.53	17.06	49.57
PRESERVED $PO^{14}C$	8.87	29.69	57.87
PHYTOPLANKTON TO PRESERVED $PO^{14}C$ RATIO	0.74	0.57	0.86

Table 3-7: Contributions of carbon (μg C l^{-1}) by various taxa to non-bloom POC pool over time as estimated from ^{14}C track autoradiography and cell abundance data.

	NON-BLOOM ENCLOSURE		
TAXONOMIC GROUP	DAY 1 (21.0 h)	DAY 2 (45.0 h)	DAY 3 (66.0 h)
chlorophyta	5.05	5.34	5.49
cryptophyta	0.10	0.15	0.24
PHYTOPLANKTON CARBON TOTAL	5.15	5.49	5.73
PRESERVED PO^{14}C	17.11	22.63	28.25
PHYTOPLANKTON TO PRESERVED PO^{14}C RATIO	0.30	0.24	0.20

DISCUSSION

Large *in situ* enclosure experiments have been shown to be a very useful way to study natural phytoplankton communities for extended periods of time while minimizing containment effects (Jahnke *et al.* 1983; Kattner *et al.* 1983; Kuiper *et al.* 1983; Aksnes *et al.* 1985; Reynolds *et al.* 1985). The relative stability of concentrations of chlorophyll *a*, POC, PON, and ratios of C:N and C:Chlorophyll *a* over the course of the experiments indicated that containment effects were negligible in the present study. The use of enclosures as balanced ecosystems allows measurements of energy flows *in situ* rather than by extrapolating information obtained from artificial environments in laboratory studies. Accurate measurements of primary production and energy flow during bloom and non-bloom conditions are essential for the implementation of trophodynamic models to estimate potential fishery production in coastal Newfoundland waters.

4.1. SESTON

The mean concentrations recorded for POC in bloom and non-bloom enclosures were representative of levels recorded for coastal waters with similar corresponding levels of chlorophyll *a* (Takahashi *et al.* 1978; Hollibaugh and Booth 1981; Eilertsen and Taasen 1984). Increases in bloom enclosure chlorophyll *a* concentration over the time course of the experiment, coupled with stable POC measurements, suggest that increasing amounts of carbon were being shunted into phytoplankton biomass.

Carbon to chlorophyll *a* ratios, and concentration of adenosine triphosphate (ATP) have been used to estimate phytoplankton biomass (Steele and Baird 1985; Marra *et al.* 1981; Valiela 1984). My Chl *a*-based calculations indicate that 65%

of the bloom and 22% of the non-bloom seston was composed of living phytoplankton carbon, similar to levels reported for Hawaiian coastal waters (Laws *et al.* 1984). This is probably an underestimate of the live carbon as both Steele and Baird (1965) and Banse (1974) suggest that elevated levels of detrital material in samples decrease the accuracy of this method of prediction, as the estimates include other living carbon sources such as bacteria in addition to phytoplankton.

4.2. COMMUNITY PRIMARY PRODUCTION

4.2.1. EFFECTS OF INCUBATION DURATION

Standard ^{14}C incubations of up to 24 h duration do not appear to be sufficient to measure primary production accurately during both bloom and non-bloom periods. An examination of the net carbon fixation per hour for various intervals throughout the first day of the experiments (Table 4-1) reveals that it would be difficult to preselect a short incubation period that would accurately reflect the daily rates. Rates varied an order of magnitude between 2-hour intervals within each experiment and varied 2-3 fold even with 4-hour and 6-hour intervals. Thus it seems that full day incubations are necessary to integrate the unpredictable diurnal variations. The analysis of the non-bloom experiment clearly demonstrates that full day estimates can still be in considerable error when the phytoplankton carbon pools are saturating to a measurable degree. In this case, the corrected production estimate of 120 μg C l^{-1} was three times the uncorrected flux estimate. The daily accumulation of label in the non-bloom experiment can be interpreted as the net daily primary production, while the corrected estimate represents the gross daily primary production. The difference between these two values is largely due to respiration (see below). Recognition of saturation effects requires that experiments be run for a period of several days so that the pool size and turnover time can be determined. Incubations longer than one day will most likely include measurable fluxes of label by community components further up the food chain, and so it becomes necessary to discuss production and respiration at the community or biomass level.

Table 4-1: Primary production estimates calculated for various intervals during-day one in bloom and non-bloom enclosures.

	PRIMARY PRODUCTION	
	BLOOM ENCLOSURE	NON-BLOOM ENCLOSURE
INCUBATION DURATION	PRODUCTION $\mu g\ C\ l^{-1}h^{-1}$	PRODUCTION $\mu g\ C\ l^{-1}h^{-1}$
TWO HOUR		
0530-0730	—	0.55
0730-0900	3.16	2.85
0900-1130	2.44	1.05
1130-1330	3.38	4.46
1330-1530	9.92	—
1530-1730	2.32	5.15
1730-1930	1.73	5.04
FOUR HOUR		
0530-0930	1.52	1.70
0930-1330	2.96	2.75
1330-1730	6.11	2.43
SIX HOUR		
0530-1130	1.86	1.48
1130-1730	5.21	3.11
FOURTEEN HOUR		
0530-1930	3.31	2.89

* NO NET ACCUMULATION OF CARBON

Short-term incubations ($\leq$ 1 d) do not allow the researcher to adequately assess whether or not corrections for isotope saturation should be applied or even if such saturation has taken place. Estimates of primary production made in the absence of such information will tend to underestimate actual production. This may account for the inability of Mills and Fournier (1979) to explain observed benthic and pelagic fish production through the application of trophodynamic models in the Scotian Shelf region using conventional ^{14}C production data. Corrected primary production estimates for bloom and non-bloom enclosures were approximately 100 $\mu g\ C\ l^{-1}\ d^{-1}$, exceeding the maximum value of 82 $\mu g\ C\ l^{-1}\ d^{-1}$ recorded for the highly productive shelf-break region of the Grand Banks (Hollibaugh and Booth 1981) using conventional tracer techniques and shipboard incubations. The low biomass, non-bloom community maintained a rate of primary production equal to that of the bloom assemblage which had a much higher phytoplankton biomass.

4.2.2. CHLOROPHYLL-SPECIFIC RATES OF PRODUCTION

Although absolute primary production estimates were similar in both experiments they differed markedly when expressed in terms of rate per unit Chl *a* ($\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$). Primary production during the diatom bloom ranged from 5-10 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$ while non-bloom values were as high as 25 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$. Platt and Subba Rao (1975) and Parsons *et al.* (1977) have summarized literature Chl *a* specific primary production estimates ranging from 0.1 to 98 mg C mg Chl $a^{-1}\ h^{-1}$. Jahnke *et al.* (1983) and Reynolds *et al.* (1985) recorded rates of 5.7 and 5.8 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$ respectively for diatom dominated phytoplankton communities in marine and freshwater systems. Laws *et al.* (1984) found production estimates as high as 15.5 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$ in near shore Hawaiian communities with 54-56% nanoplankton biomass, and Aksnes *et al.* (1985) recorded rates as high as 25.1 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$ in Norway, although the community composition was not clear. Hollibaugh and Booth (1981) indicated that specific primary production estimates ranged from 1.5 to 12.0 $\mu g\ C\ \mu g\ Chl\ a^{-1}\ h^{-1}$ in the Grand Banks area in 1980, the highest being measured in

August and the lowest in November. The higher photosynthetic efficiency of the non-bloom community in the current study may be partially due to its being in better condition in that its C:N ratio of 9.2:1 was closer to that typical for healthy phytoplankton (6.6:1, Redfield *et al.* 1963; and 7.7:1, Healey 1975) than was the ratio of the bloom community (13.1:1).

4.2.3. COMMUNITY RESPIRATION

Nightly loss of ^{14}C was observed in both bloom and non-bloom enclosures (Figures 3-5 and 3-6). The close correspondence between particulate and total organic radiocarbon concentrations indicates that the loss was due to community respiration rather than to dissolved organic carbon production. An estimate of the respiration rate can be generated for the non-bloom enclosure by subtracting the observed daytime radiocarbon accumulation (net production) from the turnover-corrected (gross primary production) value of 120 $\mu g\ C\ l^{-1}$ yielding a difference of 79.5 $\mu g\ C\ l^{-1}$, equivalent to respiration rate of 5.7 $\mu g\ C\ l^{-1}\ h^{-1}$ during the 14 hour daylight period. A second estimate can be generated from the rapid decline in particulate radiocarbon during the first sampling interval after dusk on day 1. This yields a community respiration rate of 4.6 $\mu g\ C\ l^{-1}\ h^{-1}$. Either of these rates, if maintained over the 10-hour dark period, would consume more than the total net production of the previous day which is consistent with the observation of stable Chl *a* and POC concentrations. The slower rate of radiocarbon decline later during the first night (Figure 3-6) might indicate either that the respiration rate had declined or, alternately, that an increasing proportion of unlabelled substrate was being consumed (or both). Rivkin (1985) also suggests that the majority of the loss at night is due to respiration with only about 10% being due to cell leakage. Respiration would be expected to be greater during the non-bloom experiment both due to higher temperature (14.5 °C vs. 6 °C) and due to the dominance of phytoflagellates as compared to diatoms during the bloom. Banse (1976), Burris (1977), and Smith (1977) have observed higher respiration rates in motile phytoplankton species than in non-motile forms.

4.3. SPECIES SPECIFIC PRIMARY PRODUCTION

Track autoradiography-based measurements of carbon uptake and pool size at the cellular level revealed that similar taxa accumulate more radioactive label (w/v) under bloom conditions than in non-bloom conditions. Phytoplankters also turned over cellular carbon pools faster and thus saturated faster in the non-bloom enclosure than in the bloom enclosure. The use of track autoradiography allowed the assessment of how large the metabolically active cellular carbon pool was on a species level and how fast that pool was turned over or labelled.

Nanoplankters (chlorophytes and cryptomonads) common to both bloom and non-bloom enclosures incorporated about twice as much ^{14}C into cellular carbon in the bloom experiment as did cells in the non-bloom enclosure (Figures 3-9 and 3-10). The proportion of the cellular volume labelled by the end of the bloom incubation was approximately 10.5%, about that expected for cells in logarithmic growth in culture (Cushing *et al.* 1958b and Mullin *et al.* 1966). The same cells in the non-bloom enclosure were nearly saturated by the second day of incubation at 4.5% of the cell volume, a level only half that observed in the bloom enclosure. The non-bloom cells nevertheless were maintaining high rates of primary production.

Flagellated nanoplankters are found year around in the near-shore Labrador current water (per. observ.), unlike many of the non-motile diatom species found only during bloom conditions, and therefore undoubtedly contribute the major portion of total annual primary production.

4.4. PHYTOPLANKTON CONTRIBUTIONS TO TOTAL POC

The importance of being able to determine specific carbon contributions to the total POC is that it permits identification of the major sources of energy for the food chain. Track autoradiography-based μg C cell^{-1} estimates used in conjunction with cell abundance in cells ml^{-1} yielded total C ml^{-1} estimates which were lower than preserved filter PO^{14}C values in both bloom and non-bloom enclosures (Tables 3-6 and 3-7). The summation of microscopically identifiable carbon sources accounted for up to 86% of total PO^{14}C during the bloom but

only a maximum of 30% in the non-bloom enclosure. The track autoradiography-based estimate of particulate radiocarbon per unit water volume was found to be in very good agreement with the filter PO^{14}C, however, indicating the isotope was in unidentifiable small particulates or possibly colloidal forms on the slide. Beta emissions from damaged cells, loose cell contents, or bacteria could account for the discrepancy in carbon estimates. This strongly suggests that energy flow to higher trophic levels may not be solely through a classical algae-grazer food chain during non-bloom conditions.

Pomeroy and Deibel (1986) have documented the suppression of bacterial activity in cold Newfoundland waters. It may be that reduced rates of breakdown permit the small particulates to persist long enough to play an important role in maintaining energy flow to higher trophic levels.

4.5. CONCLUSIONS

The use of long-term, large enclosure, *in situ* ^{14}C incubations of natural phytoplankton populations allows more accurate determination of marine primary production. Near-shore primary production estimates in Newfoundland waters indicate potential carbon sources for energy transfer to metazoan consumers which in turn could provide a food base for the coinciding summer recruitment of larval fish.

Incubations longer than one day are required to ascertain whether or not production estimates are complicated by the saturation of the metabolic pool. The standard, 1 day incubation technique yielded a primary production estimate during the non-bloom period that was only 34% of the total carbon flux. Corrected primary production estimates made in both bloom and non-bloom conditions in coastal waters were both higher than previous values recorded for the highly productive shelf-break region of the Grand Banks. There are insufficient data to determine the generality of these values and to thereby evaluate whether or not previous Grand Banks data should be corrected.

The maintenance of high rates of carbon flux by relatively small densities of nanoplankton during non-bloom conditions raises questions concerning the major

pathways of energy flow during much of the year. Further investigations of the production of particulate organic matter in non-bloom conditions may clarify the pathways of energy flow responsible for successful fish recruitment during periods when nutrients and phytoplankton biomass are low.

Track autoradiography allows the determination of carbon flow and cellular carbon pool sizes on a species scale in natural phytoplankton assemblages. The use of this technique enabled me to show that nanoplankton in non-bloom condition can carry out rates of primary production equal to those in bloom conditions utilizing a smaller active cellular carbon pool.

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APPENDICES

APPENDIX A

REPLICATE PARTICULATE NITROGEN AND CARBON ESTIMATES AND CALCULATED ATOMIC C:N RATIO FOR BLOOM ENCLOSURE

TIME*	NITROGEN (μg N l^{-1}) #1	#2	MEAN	CARBON (μg C l^{-1}) #1	#2	MEAN	C:N**
6.8	15.0	20.1	17.52	293.7	421.9	357.79	23.8
8	37.2	21.9	29.53	288.3	271.3	279.79	11.1
14.8	19.1	26.8	22.98	330.2	318.2	324.18	16.5
18.8	51.1	25.1	38.08	366.7	316.8	341.71	10.5
22.8	20.9	30.8	25.81	215.3	281.4	248.38	11.2
30.8	22.6	23.3	22.94	291.0	339.5	315.23	16.0
36.2	27.8	25.1	26.44	219.4	237.6	228.48	10.1
41.8	20.9	25.1	22.96	345.1	296.9	320.96	16.3
44.8	36.2	29.7	32.93	324.8	359.4	342.08	12.1
52.8	45.2	50.0	47.60	315.3	—	315.30	7.2
54.8	30.9	39.7	35.29	292.4	322.4	307.39	10.2
59.8	34.8	29.7	32.23	292.4	411.9	352.14	12.7
65.8	26.4	30.4	28.42	336.9	305.4	321.17	13.2
68.8	33.7	29.0	31.36	316.7	340.9	328.79	12.2
MEAN			29.585			313.099	13.11
s.e.			2.035			9.993	1.07
N			14			14	14

*ELAPSED TIME (hours) AFTER C-14 INOCULATION
**CALCULATED AS RATIO OF MEANS

APPENDIX B

REPLICATE PARTICULATE NITROGEN AND CARBON ESTIMATES AND CALCULATED ATOMIC C:N RATIO FOR NON-BLOOM ENCLOSURE

TIME*	NITROGEN ($\mu g\ N\ l^{-1}$) #1	#2	MEAN	CARBON ($\mu g\ C\ l^{-1}$) #1	#2	MEAN	C:N**
0.0	35.5	22.9	29.19	—	—	—	—
7.0	33.7	18.3	26.01	165.3	264.2	214.76	9.6
9.0	26.7	—	26.74	189.7	—	189.70	8.3
13.0	18.4	19.0	18.72	146.4	279.8	213.11	13.3
19.0	31.3	18.3	24.79	157.2	164.8	160.99	7.6
23.0	24.0	17.5	20.74	155.9	177.5	166.70	9.4
31.0	27.5	17.9	22.71	157.2	173.3	165.25	8.5
36.0	35.1	25.8	30.45	146.4	181.8	164.11	6.3
42.0	29.9	20.8	25.35	177.5	154.8	166.15	7.6
47.3	23.3	17.6	20.44	149.1	306.8	227.96	13.0
53.2	35.5	16.2	25.82	151.8	157.7	154.74	7.0
60.0	31.6	19.7	25.68	141.0	271.3	206.15	9.4
69.0	22.6	20.4	21.52	165.3	286.9	226.12	12.3
77.0	30.3	21.2	25.70	180.2	230.1	205.14	9.3
81.0	30.3	20.4	25.34	165.3	183.2	174.28	8.0
MEAN			24.617			188.226	9.25
s.e.			0.837			7.058	0.58
N			15			14	

* ELAPSED TIME (hours) AFTER C-14 INOCULATION
** CALCULATED AS RATIO OF MEANS

APPENDIX C

CHLOROPHYLL A REPLICATES AND MEANS OVER TIME FOR BLOOM AND NON-BLOOM ENCLOSURES

BLOOM ENCLOSURE (μg Chl a l^{-1})				NON-BLOOM ENCLOSURE (μg Chl a l^{-1})			
TIME*	#1	#2	MEAN	TIME*	#1	#2	MEAN
0.0				0.0	0.29	0.00	0.290
6.8	0.55	0.77	0.661	7.0	0.15	0.18	0.167
8.9	1.10	1.26	1.179	9.0	0.58	0.56	0.572
11.0	0.65	0.96	0.808	11.0	0.03	0.19	0.113
12.8	0.93	1.36	1.140	13.0	0.18	0.18	0.181
14.8	1.63	0.80	1.214	15.0	0.30	0.47	0.386
16.8	0.90	1.45	1.175	17.0	0.18	0.58	0.382
18.8	0.59	0.96	0.779	19.0	0.04	0.18	0.108
20.8	0.99	1.16	1.077	21.0	0.24	0.38	0.308
22.8	0.92	0.96	0.940	23.2	0.16	0.35	0.255
25.8	0.98	1.36	1.170	26.0	0.26	0.36	0.310
28.8	0.87	1.16	1.013	31.0	0.18	0.18	0.182
30.8	1.03	0.96	0.999	33.0	0.18	0.36	0.267
32.8	1.27	1.55	1.409	36.0	0.14	0.18	0.163
36.2	0.75	1.06	0.906	39.0	0.27	0.38	0.323
38.8	0.99	1.75	1.370	42.0	0.19	0.18	0.186
41.8	0.87	0.57	0.720	45.0	0.26	0.43	0.342
44.8	1.00	1.45	1.228	47.0	0.10	0.18	0.142
46.8	0.85	0.87	0.857	50.5	0.26	0.44	0.347
49.8	1.14	1.84	1.492	53.2	0.16	0.38	0.270
52.8	0.94	1.55	1.248	56.5	0.21	0.38	0.294
54.8	1.00	1.65	1.326	58.0	0.37	0.38	0.372
56.8	1.47	1.94	1.707	60.0	0.24	0.18	0.211
59.8	1.54	1.75	1.644	63.0		0.39	0.390
62.8	0.94	1.84	1.404	66.0	0.28	0.20	0.240
65.8	1.02	1.36	1.189	69.0	0.09	0.19	0.142
68.8	0.93	1.55	1.243	71.0	0.14	0.47	0.308
				74.0	0.23	0.36	0.292
				77.0	0.38		0.298
				79.0	0.26	0.39	0.324
				81.0	0.21	0.38	0.295
MEAN			1.1461				0.2729
s.e.			0.0529				0.0179
N			26				31

* TIME ELAPSED (hours) AFTER C-14 INOCULATION

APPENDIX D

CELL ABUNDANCE AND C-14 TRACK AUTORADIOGRAPHY BASED ESTIMATES OF CARBON CONTENT OVER TIME FOR *NITZSCHIA SERIATA* IN BLOOM ENCLOSURE

TIME*	CELLS PER ML	PG CARBON PER CELL
6.8	3.8	0.36
8.9	5.5	0.53
11.0	6.2	0.62
12.8	8.6	1.39
14.8	8.3	2.52
16.8	6.5	2.57
18.8	7.8	4.23
20.8	10.0	6.54
22.8	8.6	10.01
25.8	10.1	5.48
28.8	8.8	5.14
30.8	8.7	5.45
32.8	8.2	5.96
36.2	6.0	6.92
38.8	10.7	3.44
41.8	11.3	5.81
44.8	10.8	5.58
46.8	—**	6.09
49.8	11.5	8.62
52.8	13.9	10.35
54.8	11.9	10.84
56.8	13.9	—**
59.8	8.9	—**
62.8	11.1	11.47
65.8	8.8	24.48
68.8	12.7	—**

* TIME ELAPSED (hours) AFTER INOCULATION WITH ^{14}C
** HYPEN INDICATES MISSING DATA

APPENDIX E

COMPARISON OF RADIOCARBON RETAINED ON FILTERS FROM FRESH VERSUS LUGOLS PRESERVED SAMPLES OVER TIME FOR BLOOM AND NON-BLOOM ENCLOSURES.

BLOOM ENCLOSURE (μg C l^{-1})			NON-BLOOM ENCLOSURE (μg C l^{-1})		
TIME*	FRESH	PRESERVED	TIME*	FRESH	PRESERVED
6.8	0.48	0.08	7.0	2.81	0.30
8.9	0.00	5.02	9.0	3.92	0.86
11.0	6.58	2.02	11.0	9.62	3.01
12.8	11.66	3.85	13.0	11.72	3.67
14.8	18.42	6.61	15.0	20.65	8.75
16.8	38.26	8.87	17.0	20.08	9.22
18.8	42.89	10.48	19.0	30.38	12.56
20.8	46.34	11.47	21.0	40.47	17.11
22.8	33.37	10.43	23.2	40.46	12.74
25.8	39.33	10.64	26.0	27.31	12.76
28.8	28.87	9.13	31.0	25.44	13.78
30.8	32.83	11.58	33.0	40.08	24.09
32.8	34.08	11.62	36.0	33.19	16.92
36.2	47.54	15.43	39.0	26.05	14.61
38.8	70.76	20.98	42.0	33.52	17.31
41.8	107.82	29.69	45.0	45.95	22.63
44.8	130.97	35.98	47.0	51.81	21.72
46.8	133.86	34.78	50.5	49.14	23.88
49.8	136.90	36.75	53.2	41.41	18.84
52.8	128.93	44.03	56.5	26.96	14.15
54.8	122.47	44.17	58.0	38.97	17.88
56.8	111.57	39.50	60.0	31.95	18.11
59.8	121.00	52.69	63.0	52.64	28.40
62.8	101.22	38.89	66.0	55.07	28.25
65.8	171.15	57.87	69.0	57.30	27.21
68.8	237.81	86.49	71.0	60.49	32.33
—	—	—	74.0	52.89	31.99
—	—	—	77.0	41.11	24.77
—	—	—	79.0	41.86	23.97
—	—	—	81.0	49.87	28.09

* TIME ELAPSED (hours) AFTER INOCULATION WITH ^{14}C