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FIRST OBSERVATIONS OF THE NATURE OF SEDIMENTING PARTICLES IN THE GULF OF ST. LAWRENCE, CANADA

Thesis
by

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Abstract

Sediment trap samples have provided the first direct observations of the sinking particles that account for the export of material out of the photic zone in the Gulf of St. Lawrence and their relationship to variations in the trophic regime. Particles were collected at several sites over 24-hour periods using 0.03m^2 (collecting surface) and 0.5 m^2 free-drifting sediment traps at 50 and 150 m. Total mass flux varied widely (80-1500 mg/m^2/d), as did carbon flux (16-300 mgC/m^2/d). Small cylinders consistently over sampled with respect to big cylinders, regardless of depth or drifter design. Also, 6-month time-series were obtained with a moored, 0.125 m^2 trap at two sites. In the Anticosti Gyre, time-series fluxes were consistent with those obtained from the large drifting trap (means: 480 mg dry wt/m^2/d; 39 mgC/m^2/d), and with independently measured sediment accumulation rates. Numeric fluxes of phytoplankton cells were similar to those found in moderately productive ocean margins during the April 1994 bloom, but otherwise resembled those from oligotrophic regimes. Fecal pellet numeric fluxes, in contrast, were always high, similar to other continental margins. The composition of the material collected by the small and large traps is a good indicator of the changing trophic regime in the water column. Relative numeric abundances suggest three distinctly different periods. A "bloom" period (represented by April 1994, but including a weaker late-fall bloom over a shelf valley), when a variety of centric and pennate diatom cells made up 70-95% of the particle numbers; a transitional or "post-bloom" period (June 1994), when phytoplankton were less abundant, pennate forms were scarce and a single species dominated the centric diatoms; and a "non-bloom" period (May to Dec., 1993) when fecal pellets and microzooplankton accounted for greater numbers than the phytoplankton cells, including abundant dinoflagellates. The time-series Anticosti Gyre trap showed continued large-particle settling throughout the winter with total mass and carbon fluxes similar to those found in the ice-free seasons. The most frequent fecal pellets were 50-109 µm diameter compact and loose rods, produced by the dominant calanoid copepods. Large macrozooplankton fecal pellets occurred only sporadically. Many pellets <49 µm were collected in December 1993, probably produced by *Microcalanus*, which was unusually abundant at this time. Oval pellets occurred over a broad range of diameters, suggesting multiple origins. The particulate organic carbon (POC) and the C contribution of the different types of particles have been analyzed for free-drifting sediment traps. Two trap models only were used in 1993-1994: small traps at 50 m an and larger traps at 50 and 150 m. Absolute mean fluxes of POC (42– 149 mg C m^{-2} d^{-1} on large and small traps respectively), of C attributed to fecal pellets (6 -60 mg C m^{-2} d^{-1}) and of C attributed to phytoplankton (3.2 – 42.9 mg C m^{-2} d^{-1}) were all in the same range as those encountered in regions of moderate productivity. Fecal pellets were the major component of this flux, with an important contribution of microzooplankton, particularly during the summer of 1994. The phytoplankton contribution to POC flux was lightly smaller than the fecal pellets contribution. The identification of algal groups that are part of this flux led to recognition of the three trophic regimes already identified from water column studies and from the numeric fluxes in this study: (1) a "bloom" period, when the diatoms were dominant during spring, (2) "non-bloom" period, a longer interval, which was dominated by dinoflagellates and (3) a transition “post-bloom” period during the summer. Although the contribution of marine snow was estimated, its real importance in the vertical flux of POC remains uncertain. The bulk of the settling material produced by the pelagic food web in the Gulf appears to be of zooplanktonic origin. mainly fecal pellets and abundant microzooplankton).. Much of the organic matter produced photosynthetically must thus be transformed by heterotrophos before escaping from the surface and intermediate waters in this region. The vertical flux of recognizable C at the GSL is dominated by components of animal origin.

Resumen

Se presentan las primeras observaciones acerca de las partículas en sedimentación que forman parte del material exportado de la zona fótica en el Golfo de San Lorenzo (Canadá, GSL) obtenidas mediante trampas de sedimento, así como sus relaciones con las variaciones del régimen trófico. Las partículas fueron recolectadas en varios sitios y periodos del año durante muestreos de 24 horas con trampas de libre deriva de 0. 03 m^2 y 0.5 m^2 (superficie de recolecta) a 50 y 150 m de profundidad. Los flujos de masa total variaron ampliamente (80-1500 mg/m^2/d), así como los flujos de carbono (16-300 mgC/m^2/d). Las trampas pequeñas recolectaron consistentemente más material (16-300 mgC/m^2/d) que las grandes, sin importar la profundidad o el diseño de deriva. Adicionalmente se obtuvieron seis meses de datos de series de tiempo con una trampa de 0.125 m^2 anclada en dos localidades. En el Giro de Anticosti los flujos estimados de series de tiempo fueron consistentes con los obtenidos mediante las trampas de libre deriva (flujos promedios: 480 mg/m^2/d; 39 mgC/m^2/d peso seco) y con las tasas de acumulación de sedimento medidas independientemente. Los flujos numéricos del fitoplancton durante el florecimiento de abril-1994 correspondieron con los que se presentan en márgenes oceánicos moderadamente productivos y en regímenes oligotróficos. Los flujos numéricos de pelotillas fecales fueron siempre elevados y similares a los flujos de otros márgenes continentales. La composición del material recolectado por las trampas, pequeña y grande, fue un buen indicador del cambio de régimen trófico en la columna de agua. Las abundancias numéricas sugieren claramente tres distintos periodos: un periodo de "florecimiento" (representado por las muestras de abril de 1994, pero que incluyó un florecimiento más débil de fines de otoño en un valle de plataforma), donde una variedad de diatomeas pennales y centrales constituyó 70-95% del flujo numérico; un segundo periodo de transición o "post-florecimiento"(junio 1994), durante el cual el fitoplancton fue menos abundante, las formas pennales fueron más escasas y una sola especie dominó las diatomeas centrales; y un periodo final de "no-florecimiento" (mayo a dic., 1993) a lo largo del cual las pelotillas fecales y el micro zooplancton presentaron mayores flujos numéricos que las células fitoplanctónicas, incluyendo abundantes dinoflagelados. Las series de tiempo de la trampa del Giro de Anticosti presentaron sedimentación continua de grandes partículas a través del invierno, con flujos totales de masa y carbono similares a los flujos de los periodos libres de hielo. Las pelotillas fecales más frecuentes fueron las compactas y las no compactas de 50-109 µm de diámetro, producidas por copépodos calanoideos dominantes. Las pelotillas ovales presentaron un intervalo amplio de diámetros, sugiriendo múltiples orígenes en el zooplancton. Se analizó en el material de 32 trampas de libre deriva para determinar el carbono orgánico particulado (COP) y la contribución de carbono de los diferentes tipos de partículas. El intervalo promedio de los flujos absolutos del COP fue (42-149 mg C m^{-2} d^{-1} en las trampas grandes y pequeñas respectivamente), los flujos de C atribuido a las pelotillas fecales (6 -60 mg C m^{-2} d^{-1}) y los flujos de C atribuidos al fitoplancton (3.2– 42.9 mg C m^{-2} d^{-1}) estuvieron todos en el mismo intervalo que los encontrados en regiones de productividad moderada. Las pelotillas fecales fueron el principal componente de este flujo, con una contribución importante del microzooplancton particularmente durante el verano de 1994. La contribución del fitoplancton al flujo del COP fue ligeramente menor que la de pelotillas fecales. La identificación de grupos de microalgas que fueron parte de este flujo, confirman la presencia de los tres regímenes tróficos ya identificados en estudios de la columna de agua y por flujos numéricos en este mismo estudio señalados arriba. No obstante que la contribución de la nieve marina fue estimada, su importancia real en el flujo vertical del COP permanece incierta. La mayor parte del material en sedimentación producido por la cadena trófica pelágica en el GSL parece ser de origen zooplanctónico. Gran parte del material orgánico producido fotosintéticamente, debió haber sido trasformado por los heterótrofos antes de escaparse de las aguas intermediarias y de superficie. El flujo vertical de C reconocible fue dominado por componentes de origen animal.

CHAPTER I

GENERAL INTRODUCTION

CHAPTER I -General Introduction

1.1 The global marine carbon cycle

The global carbon cycle is one of the earth's most important biochemical cycles, because it directly links carbon from its most basic inorganic forms to its most complex forms in living organisms. This cycle has been studied for some time. However, it was not until the end of the 1950s, with the monitoring at Mauna Loa volcano, Keeling and Whorf (2005, http:cdiac.esd.ornl.gov/trend/CO2/sio-mlo.htm)[1] that the worldwide community began to be aware of the rapid rise in atmospheric $CO_{2.}$ The study of this cycle has now attracted worldwide attention, since CO_2 is the principle greenhouse gas it by reason of its potential climatic consequences for global warming, a phenomenon of great significance for the future of the world's population

Berger (1992) demonstrated a strong correlation between the increase of atmospheric CO_2 and the growth of the human population between 1880-1990. The increase of CO_2 in the atmosphere due to anthropogenic activities represents only one of the factors effecting this global cycle. However, the atmospheric increase has served to alert the world's scientific community that there still is a profound lack of knowledge about the global carbon cycle. Even basic notions such as the magnitude of the reservoirs, the fluxes of carbon between interconnected Air-Ocean-Land systems and the processes underlying the carbon cycle are poorly understood.

[1] (last consult 6 Sep/2005).

As a result of these uncertainties, the governments of the industrialized nations financed diverse international programs that are still conducting operations and investigations. Some of these international programs focus their efforts on the carbon cycle as it relates to the marine environment. Some of these programs have terminated, while others continue under different names and include other stated objectives, but still remain focused on the marine carbon cycle. Their purpose is to understand the primary processes that control the form, distribution of the reservoirs and fluxes of oceanic carbon, while at the same time integrating the effects of human activity. Some of these programs are:

1) The U.S. government's National Oceanic and Atmospheric Administration (NOAA) has a dedicated section for investigation for the global carbon cycle. The National Oceanic and Atmospheric Administration-Carbon Global Cycle (NOAA-CGC) itself operates several programs, Pacific Marine Environmental Laboratory Carbon Dioxide Program (PMEL CO_2) in the Pacific Ocean and the Atlantic Oceanographic and Meteorological Laboratory (AOML) in the Atlantic Ocean.
2) The U.S. sponsored program Joint Global Ocean Flux Study(JGOFS) and International Geosphere-Biosphere Programme has generated valuable and extensive information with large scale sub-programs collecting time series in the Atlantic: Bermuda Atlantic Time-Series Study (BAT), in the Pacific: Hawaii Ocean Time-series (HOT) and investigations in the Antarctic with the project Antarctic Environment and Southern Ocean Process Study (US-JGOFS AESOPS):
3) The European project: Atlantic Network of Interdisciplinary Moorings and Time-series for Europe(ANIMATE)
4) South America project: Carbon Retention In A Colored Ocean Project (CARIACO), among others.

The US program (JGOFS) began in 1987. It has been one of the most ambitious oceanic bio-geochemical investigations carried out in the last decades in that it has included researchers from more than 20 countries, with the principle objective to understand the processes that control the carbon cycle and associated elements in the

ocean. A sub program of this is CJGOFS, which was implemented by the Canadian government. The positioning of this thesis research project in the particular context of the CJGOFS sub-program and in the cycle of oceanic carbon will be explained later. I first discuss some background information on the main fluxes and the carbon cycle in the marine environment.

According to Bice (2001, (http:www.geos.psu.edu/~dbice/DavesSTELLA/carbon/carbon-intro.htm)[2] if we consider the carbon cycle to be in steady state and take into account the measurements made just before the industrial revolution, the major carbon fluxes in the marine environment include:

1) the absorption of CO_2 by cold surface waters (90 Gt C /m^2/year);
2) the liberation of CO_2 from warm surface waters (90 Gt C /m^2/year);
3) the sinking of carbon towards the ocean depths and its return transport towards the equator through the formation of cold surface waters near the poles (96.2 Gt C /m^2/year);
4) the vertical advection of carbon from the deep waters towards the surface by means upwelling (105. 2 Gt C /m^2/year); while the less fluxes include:
5) the downward transport of carbon by the biological pump, i.e. the sinking of particulate carbon brought about by activities of the biota of cold waters (4 GtC m^2/year) and of warm waters (6 GtC /m^2/year),
6) the horizontal advection transports warm surface water and carbon towards the poles (10 GtC /m^2/year),
7) the deposition of carbon onto the sea floor and subsequent storage in sedimentary rock (0.6 GtC /m^2/year). The largest carbon reservoirs are found in the deep oceans (38,000 Gt C) and deposits in sedimentary rocks (1,000,000 Gt C).

It is not possible here to do a complete compilation of the historical changes in carbon in the marine environment since the industrial revolution through present time to demonstrate trends or patterns. However, it is possible to compile a partial summary of recent observations and important results produced by the international JGOFS program in relation to the processes that control the oceanic carbon cycle, as reported in the final

[2](Last consult 6 Sep/2005).

USJGOFS report, Buesseler *et al* (2001, http:/usjgofs.whoi.edu/images/ jgofs_brochure.pff)[3]. The results of this report were derived from a group of multidisciplinary investigations. This report includes time series sets from the Bermuda (BATS) (Deuser and Ross, 1980; Deuser *et al.,* 1981; Michaels *et al.,*. 1994; Bates *et al*., 1996; Conte *et al*., 2001; Steinberg *et al,*. 2001; Bates *et al.,* 2002; Gruber *et al.,* 2002) and Aloha in Hawaii (HOT) (Bingham and Lukas, 1996; Chi swell *et al.,* 1996; Cortés *et al.,* 2001; Lukas *et al*., 2001) sites. Since 1988, these sites have supplied very complete time series data sets on seasonal fluctuations, interannual variability and decadal changes for many oceanic properties and components of the carbon system.

One of the major results presented in the last report of the US-JGOFS, Buesseler *et al* (2001, http:/usjgofs.whoi.edu/images/jgofs_brochure.pff)[3] is the finding of a similar increase of CO_2 in oceanic surface waters at he Bermuda station with that at Hawaii stations, increases that coincide with an exponential rise of atmospheric CO_2 at Mauna-Loa.

Concerning the atmosphere-ocean exchange rate, the JGOFS final report showed an important interannual variability. This between the quantity of CO_2 liberate in the Equatorial Pacific between 1995 and 1998. During “El Niño” conditions (weak winds and a reduction in upwelling) there was a reduction of more close to 0.9 – 0.2 billions of metric tons of carbon per year) in the liberation of CO_2 from surface water to the atmosphere (Inoue and Sugimura, 1992; Boutin and Etcheto, 1997; Feely *et al.,* 1997; Feely *et al.,* 1999). During normal years upwelling was particularly intense in the Central Eastern Pacific. These contributed to the liberation of 4 times or more COP to the atmosphere each year than all the other equatorial regions combined.

With the availability of long term data sets from both the Bermuda (BAT) and Hawaii (HOT) sites, Buesseler *et al.* (2001, http:/usjgofs.whoi.edu/images/jgofs_brochure.pff)[3] it has been possible to compare these data series with predictions from complex models

[3](last consult 6 Sep/2005).

that simulate the behavior of the tropical ocean belt, including the physical environment. For example, changes in the levels of chlorophyll *a* at different depths in the Bermuda site mark the beginning and end of blooming periods. The same results are obtained with a simulation model that accurately predicts the annual pattern of phytoplankton blooms at this site. (Lima and Doney, 2004).

Buesseler *et al*. (2001, http:/usjgofs.whoi.edu/images/jgofs_brochure.pff)[3] also show the results of a global oceanic model that predicts warming in oceanic surface temperature at the end of this century, if CO_2 continues to increase. The changes in temperature predicted in this model also could affect the solubility CO_2 in oceanic water. In addition, the changes in the temperatures and of the wind patterns could alter the sub-surface ocean circulation and upwelling patterns that bring nutrient rich waters to the surface. These changes could affect the structure and function of oceanic ecosystems and, in turn, the way the biologic pump operates in different regions of the ocean. Changes in the capacity of the ocean to absorb and store carbon could also affect the accumulation of CO_2 in the atmosphere.

Since most of the oceanic carbon is stored in deep water (38,000 Gt C) and sediments (1,000,000 GtC) Bice (2000, http: www.geos.psu.edu/~dbice/DavesSTELLA/carbon /carbon-intro.htm)[2] several important questions concerning the global carbon cycle need to be answered. How fast is carbon transferred from the atmosphere to the deep ocean? In what form is it transported? What processes transport it? The JGOFS final report Buesseler, (2001, http:/usjgofs.whoi.edu/images/jgofs_brochure.pff)[3] mentions that one of these processes that moves carbon to the ocean's depths is the rapid vertical export of particles, i.e. the biologic pump. The pump initiated by production of organic carbon by the phytoplankton, which constitutes the base of the oceanic food chain, utilizing CO_2

[2](Last consult 6 Sep/2005).

[3](Last consult 6 Sep/2005).

and nutrients in photosynthetic processes that form particulate organic material.

Subsequently zooplankton that at feed on phytoplankton produce large particles be it by defecation, settling moults, their own bodies at death, or by vertical migration or by other methods of aggregating smaller particles. These sinking particles transport organic material through the water column and thereby move carbon to the ocean depths. During the days to weeks that it takes these particles to reach the sea floor, many of the particles are decomposed by marine bacteria, consumed by zooplankton or by other organisms that inhabit the ocean depths.

The investigations of JGOFS attempted to understand what it is that effects the efficiency of the biologic pump, which in general is week. Buesseler, *et al*. (2001, http:/usjgofs.whoi.edu/images/jgofs_brochure.pff)[3] indicates that for each 1000 of carbon fixed by primary production at the surface of the open ocean, only 50-100 atoms reach 1000 m. Only 10 atoms are exported below 1000 m, where carbon is stored for millenniums. Only 1 atom is buried in sediments where it may be sequestered for millions of years.

Since 1989 Canada has become involved in the US JGOFS program, with a plan based on three principal foci: gaseous exchange at sea level, transformation and vertical transport of carbon in the ocean and the burial of carbon in bottom sediments. Between 1992-1995, the JGOFS program in has generally identified and characterized in various oceanic regions the principle processes that control the oceanic carbon cycle. This was accomplished through large-scale observations and measurements in various oceanic basins (Equatorial Pacific and North Pacific Sub-Artic, Central Atlantic, NW Atlantic and Arabian Sea), but these processes were specifically identified and characterized for the Canadian continental shelf and slope, including the Gulf of Saint Lawrence (GSL).

[3](Last consult 6 Sep/2005).

The continental shelf and slope were selected for study because the surface primary production here is exported towards the continental margins and may represent approximately 50% of the total exports that come from oceanic waters. In addition, the sediments of the continental margins are preferential sites for the deposition of organic material of terrestrial origin, Johnson and Nightingale (1994, htt:/is.dal.ca/%7Ebjohnson /info.3htm)[4]. It has been estimated that globally more than 80% of the mineralization of sedimentary organic material and more than 80% of burial of organic material takes place along the length of the continental margins, thus making these one of the most important geographic sites for carbon sequestration in the cycle of global carbon, Johnson and Nightingale (1994, htt:/is.dal.ca/%7Ebjohnson/info.3htm)[4].

As previously mentioned, one of the ways by which carbon is exported towards the ocean depth is the biologic pump. This mechanism doesn't involve the largest carbon fluxes. But, it implicates physical, chemical and biological processes throughout the length of the water column. This make the biologic pump an important aspect of the oceanic carbon cycle and also one of the most complex.

Relating changes in atmospheric CO2 to efficiency of biologic pump requires a detailed comprehension of complex trophic mechanisms by which carbon in the ocean is transformed, transported, recycled, and finally sequestered via burial in seafloor sediments. The present thesis was developed following this line of investigation.

1. 2 Previous studies and rationale for this project

An increasing number of components and mechanisms have been recognized that regulate the exportation of biogenic carbon from the ocean's surface towards the seafloor below. Noji *et al.* (1999) mentioned that these mechanisms range from the sedimentation

[4](Last consult 6 Sep/2005).

of non-grazed spring blooms to a complete chain of system-dependent processes that include the production of fecal pellets by zooplankton and the distribution of particulate carbon in the ocean, mechanisms and components just as important as the accumulation of dissolved organic carbon (DOC) in marine surface waters. For his part, Turner (2002) in his bibliographic review, mentioned that the vertical flux of fecal pellets, marine snow and sinking phytoplankton are the most important components that transport and recycle biogenic carbon in the sea. Dr. Sussumu Honjo, after years of sediment trap work in the open ocean, summarize the components most frequently observed as: “fecal pellets and aggregates as well individually, relative large particle such as planktonic phoraminiphera and diatoms.” All of these together for marine snow” (Honjo, 1997).

Other examples from the literature include: large-size phytoplankton (Legendre and Le Fèvre, 1989), fecal pellets (Longhurst and Harrrision, 1989; Noji, 1991, González *et al*., 2000); dead organisms, hard fragments nano-, micro and mesozooplankton and their excretions (Longhurst and Harrison, 1989, Silver and Gowing 1991, Prieto *et al*., 2001); aggregates of diatoms (Alldredge *et al*., 1988, Alldredge and Gotschalk, 1989; Riebesell, 1991, Alldredge *et al.*, 1993, Grossart *et al*., 1997) and aggregates of marine snow (Alldredge and Gotschalk, 1990, Alldredge *et al.,* 1995; Alldredge, 1998) and other particulate inorganics like small mineral grains, as well as particles of terrestrial origin like pollen (Romero *et al*., 2000). The nature of the materials that dominate the vertical flux of the sedimenting particles in the St. Lawrence Gulf are presented for the first time in this study.

In general, the quantitative importance of the vertical flux of POC, augmented with primary production and diminished with depth (Martin *et al*, 1987). The quantitative importance and the composition of the particles are principally determined by the structure of the planktonic trophic chain, in addition to the influence of other consumers, like as fish (e.g. Staresinic *et al*., 1983)

In oligotrophic systems (e.g. the Sargasso Sea, North Central Pacific), small size organisms dominate planktonic communities (Azam *et al.,* 1983; Fenchel, 1988; Fenchel,

2001). In these types of systems, regenerated production dominates photosynthetic carbon fixation, as phytoplankton utilize principally ammonia (NH_4) excreted by the organisms as their nitrogen source in a recycling system described as a "microbial loop". Eutrophic systems, on the other hand, use nitrate injected into systems by upwelling or mixing from below induce "New" production (Dugdale and Goering, 1976). Dominate by large phytoplankton, such as diatoms and mesozooplankton grazer, eutrophic systems are capable of producing and exporting the large particle that settle rapidly (Legendre and Le Fèvre 1989; Silver and Gowing, 1991)

In the St. Lawrence Gulf, however, Rivkin *et al*. (1996) demonstrated that these conditions aren't always fulfilled as similar carbon fluxes encountered during a blooming period as in one without a bloom. The high carbon flux associated with fecal pellets even during the non bloom condition indicated that the systems was not closed and the mesozooplankton were probably feeding on microzooplankton ciliates. This point out the need to obtain detailed information about how the trophic regime changes during the year.

Most of the studies about particle have been carried out in the open ocean and often included only a few types of particles. Although some studies reported the contribution of specific particle to the flux of POC (Honjo and Roman, 1978; Turner and Ferrante, 1979; Bruland and Silver, 1981; Fowler and Knauer, 1986; Turner, 2002), this kind of information is rare and fragmented, for both the open ocean and coastal zones. The most complete study that assigned the contributions of carbon to all components of collected trap material was that of Silver and Gowing (1991).

The present thesis was developed following this line of investigation, focusing on the nature of particles that are vertically exported from the photic zone in the Gulf of St. Lawrence (Canada). This marginal sea by itself is too small to have a significant influence on the global cycle. The results that have already been obtained here can, however be generalized for the other comparable coastal systems (Silverberg *et al*., 2000).

1.3 General Objective

The goal of this study was to present the first description of the nature of the particles that sediment in the GSL and to contribute to the understanding of the mechanisms that control their vertical flux.

1.4 Hypothesis

The composition of trap samples collected in the Gulf of San Lorenzo reflects the trophic regimes in the surface layer of the water column and thus the sinking material changes when the surface communities change.

CHAPTRE II

Nature of the particles

Sediment trap observations for the St. Lawrence Gulf and the continental margin of Eastern Canada.

2. 1 Introduction

Rapidly settling particulate matter links the surface layer to the depths of the ocean. The arrival at the sea floor of relatively fresh phytoplankton, zooplankton and organic detritus represents the principal energy and food supply for the benthos. Its subsequent mineralization drives the chemical transformations within the sediments during early diagenesis and the return of many nutrients and other metabolic products to the water column. The upward transfer of the latter, in part, determines the sustainability of elevated levels of primary productivity in the photic zone, and, over moderate time scales, such “New Production” is believed to be balanced by the loss, through sinking, of an equivalent amount of particulate carbon (Eppley and Peterson, 1979).

In detail, however, the mechanisms involved in such vertical fluxes, the timing of physical and biological events, and the dynamics of the food chain, both in the photic zone and the deeper layers, are still poorly understood and are the subject of much investigation (Smetacek *et al*., 1978; Hargrave, 1985; Bodungen, 1986; Smith, 1987; Silver and Gowing, 1991; Michaels *et al.*, 1994; Miquel *et al.*, 1994). Recent works including flow models, underline the influence of trophic dynamics on the biogenic carbon fluxes (Fasham *et al*., 1990; Moloney and Field, 1991; Legendre and Rassoulzadegan, 1996). However, this type of study requires combined knowledge of vertical fluxes and upper water column characteristics (physical and biological), which are not always available.

The study presented below is a first step in this direction. Our approach involved the detailed examination of the composition of sediment trap material and their

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relationship with the planktonic food webs of the upper water column, determined simultaneously.

Most previous work on the microscopic quantification of sediment trap particles has centered on just a number of individual components of the sedimenting material and, apart from Silver and Gowing (1991), little information is available on the entire bulk of material captured by traps. Urrère and Knauer (1981) focused their work only on the faecal material, citing the extreme difficulty of quantifying entire sub-samples in the presence of marine snow. Bathmann *et al*. (1990), when presenting their results on the relative abundance, performed microscopic counts of the number of individuals for six taxonomic groups and three classes of fecal pellets, during an annual cycle, but did not include marine snow. In this study we attempt to account for all of the material in the traps.

The quantitative estimation of vertical fluxes of either particulate carbon or of a particular type of biogenic material composing this flux is complicated by several methodological problems, including trap design and exclusion of trap material not thought to participate in the vertical fluxes ("swimmers"). We have examined these aspects for our work, to try to assess the reliability of our measurements, the first available for the eastern Canadian continental shelf and Gulf of St. Lawrence.

2.2 Methods

2.2.1 Sediment trap deployments

Three different sediment traps were used in this study (locations shown in fig. 1): a large free-drifting trap (referred to hereafter as the "large trap"); a much smaller and simpler free-drifting instrument (the "small trap"); and a 12-sample cup, moored instrument (the "time-series trap"). Moorings of 1 m^2 traps, emplaced at two deep sites in June 1993, were unfortunately lost, apparently to fishing vessels. The three sediment traps used in this study are exhibit in figure. 2.

The time-series instrument was a Technicap, model PPS-3/3, cylinder-shaped

(with a hidden basal 603 cone) sediment trap. With some differences at the Anticosti Gyre and Emerald Basin sites, the traps were placed at 150 m depth on a Kevlar or nylon mooring line, suspended from subsurface floats and anchored with a railway wheel. The carousel was programmed to rotate the acid-washed sample bottles, containing saline-preservative solution, every 10 d. The Anticosti Gyre trap was recovered a few days after the last bottle had rotated out of the cone. The acoustic release malfunctioned at the Emerald Basin site, and the instrument was only recovered after an 18-month interval through the remarkable diving operations of the crew of the submersible vessel HMCS Cormorant. Neither trap was recovered early enough for the samples to be included in the microscope analysis.

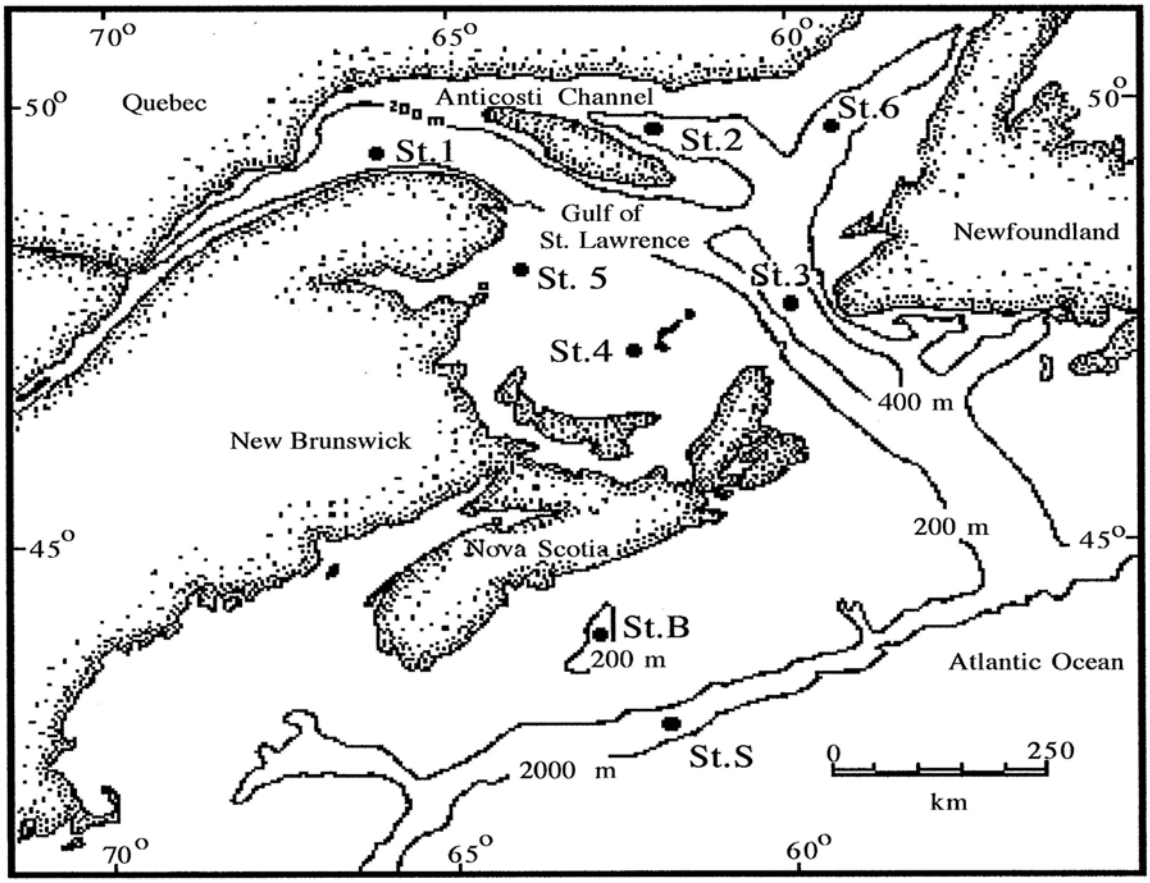

Figure 1. Chart showing the locations of the sediment trap deployments. St. 1 Anticosti Gyre (Mont-Louis); St. 2 Jacques Cartier Passage; St. 3 Cabot Strait; St. 4 Magdalene Shelf; St. 5 Miscou Channel; St. 6 Esquiman Channel; St. B Emerald Basin; and St. S Nova Scotia Slope.

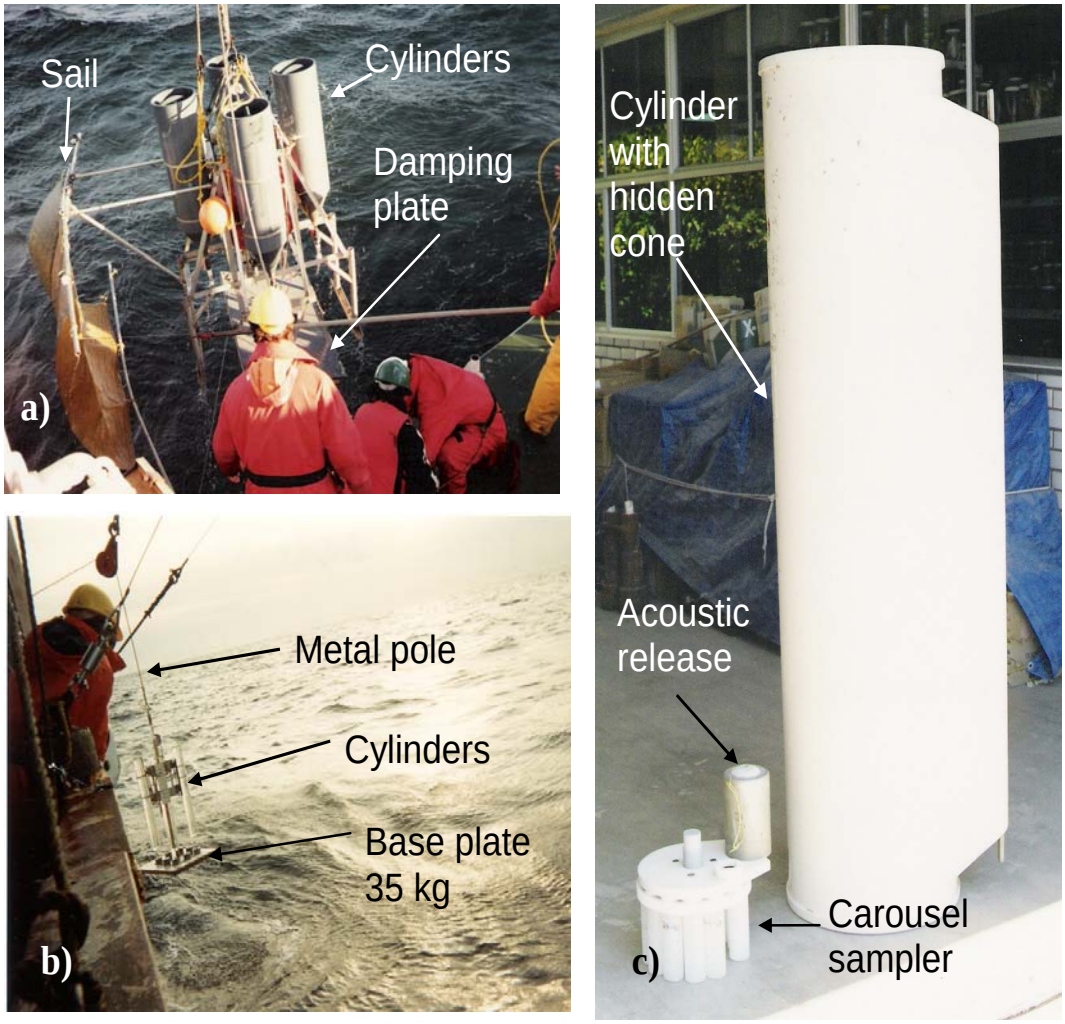

Figure 2. Sediment traps used in this study. Free-drifting were placed for 24 hrs: a) Large trap "Riki Tiki" model. b) small trap. c) Time-serie trap model PPS-3/3.

The free-drifting large trap (Silverberg *et al*., 1985) consisted of four 30 x150 cm PVC cylinders (1/8 m^2 collecting surfaces) mounted on an aluminum frame, with a wave damping plate, and aluminum tubing to extend a 2 m^2 canvas sail. It was suspended from a minimum drag surface float, with a 30 kg lead weight attached to keep the slightly positively buoyant instrument at depth.

The small trap consisted of four 98 cm-long tubes of 10.2 cm (4") I.D., attached to a metal pole with a 60 X 60 cm base plate, with a submerged weight of about 35 kg. The instrument was suspended with a 50 m polypropylene cable from a line of small

surface floats (to reduce drift) and a styrofoam buoy with mast, radar reflector and flasher. Although there was no sail, the combined vertical surface and the base plate served to reduce the pull of the surface floats.

The cylinders were filled with filtered surface seawater, supplemented by concentrated NaCl solution to achieve salinities of about 5 ppt greater than ambient deep water. The traps were lowered to 50 or 150 m depth. A radar mast and flashing light were used to track the position of the floats of each trap during sampling. The traps followed semi-elliptical courses and rarely drifted outside a 5 km radius. The large traps returned to the surface (at ~10 m/min) near dawn the following day after a time-release dropped a lead weight, closed the cylinder openings, and pivoted the damper plate. During later cruises, the large trap was simply raised as was the small trap, without triggering, using a capstan to haul the trap up through the water column. The incompressibility of cylinder water during the lifting limited measurable exchange with particles in the upper waters. The interval when the traps were open at their chosen depth represented the sampling times.

2. 2. 2 Sample retrieval, sub-sampling and other shipboard procedures

A refractometer, used to compare the salinity in the recovered samples with that of the original solution, showed that the bottom water in the collecting cylinders had not been subject to significant dilution by ambient seawater.

Concentration procedures varied with the trap being used. The Technicap samples were already concentrated in their 250 ml containers. They were removed from the carousel, sealed with a clean cover, and stored in a cold room before undergoing screening and splitting in the laboratory.

After recovery, the drifting traps were given a “rest” period of at least one hour on deck to permit any disturbed particles to resettle. In the case of the small traps, most of the overlying water in the cylinders was carefully siphoned off. About 15 cm of the cylinder water, containing the sedimented particles, were then collected into 250 ml

centrifuge bottles after passing through a 1 mm mesh nylon screen to remove copepods and other zooplankton swimmers, which were preserved in formalin. Particles that were not evidently whole zooplankton were picked off the screen and returned to the bulk sample. Of the 32 trap samples, only 12 had more than 2 or 3 organisms retained on the 1 mm screen.

The large-trap cylinders were equipped with a shut-off valve and a removable 1" ID collecting tube, containing virtually the entire trap sample. A clean Pasteur pipette was used to collect a portion of the concentrated sample (later returned) for immediate microscopic examination. The valves were then opened to flush any remaining particles which were collected into clean 2 l containers and left to settle in a refrigerator. Most of the supernatant water was later siphoned off and the samples screened and collected in centrifuge bottles.

The samples were centrifuged on board until all the material from each trap could be combined in a single container. The bulk sample was made up to a known volume and an Eppendorf pipette was used to remove a 1 or 2 ml sub-sample of the magnetically stirred suspension onto a preweighed 0.4 µm Nuclepore® filter. Washed of salts, the latter was dried and reweighed to determine the dry weight of the entire sample.

The remaining suspension was then divided into four equal volumes, using a Erez-Honjo sample splitter (Honjo and Doherty, 1988). Excess trap water was used in all manipulations to avoid subjecting the particles to a changing chemistry before final treatment. The pipette sub-sampling was repeated on each split to replicate dry weight measurements. Mercuric chloride was then added as preservative to one volume, which was sealed and stored as an archive sample. Two other splits were then centrifuged and the supernatant decanted. A final centrifugation was carried out using distilled water to remove salts and the drained sample was stored at 4°C. Subsequently, the two splits were dried, weighed and homogenized by grinding. The fourth sub-sample was split once more, providing a 1/16 fraction, preserved in 3.5% formalin, for microscopic examination.

Total mass f*lux:* The total mass flux was determined from the dry weight of the five pipetted subsamples as well as the two quarter splits. Such over determination was performed to provide increased confidence in the flux numbers, the occasionally large standard deviations indicating uncertainties inherent in this apparently simple procedure. In the case of the moored traps, the dry weight was calculated only from a pipette of the total suspension and the mass of a quarter split. The average dray weight per trap was then divided by the time the trap had sampled and the area of its collecting surface.

CHN analysis: Fifteen-mg sub-samples of the salt-free, ground dry sample were weighed on nucleopore® combusted at 950 °C and analyzed for carbon and nitrogen using a Perkin-Elmer model 1000 elemental analyzer. Triplicate analyses yielded a precision of ± 2% for carbon and ± 7% for nitrogen.

2. 2. 3 Microscopic analyses

Shipboard observations: Immediately after the collecting tubes of the big trap were removed, weather permitting, a Pasteur pipette sample of this minimally disturbed material was examined under a Zeiss stereomicroscope to take photographs and to note the general nature of the collected particles. After examination, the material was washed back into the bulk sample.

Laboratory observations: The 1/16th split was made up to a known volume, and, while stirring, a 1 ml subsample was removed to a sedimentation chamber/slide for microscopy (Hasle, 1978). Identification, counting and size measurements were performed using a Zeiss model 100 Axiovert inverted microscope, equipped with a 35 mm camera. The entire slide was examined for each sample. Six replicate pipettings were used to determine sub sampling variability in the total encountered. The average error was approximately 10% for both particle numbers and the number of taxa. Note was made of the length (longest dimension) and width or diameter (intermediate dimension) of each particle. These were then converted to projected surface area, using the simple geometric form (cylinder, sphere, rectangular box, ellipsoid) most resembling the

particle.

Because marine snow aggregate particles are subject to repeated breakdown and re-aggregation during sample preparation and because of their extended three-dimensional and tenuous nature, their surface area was determined in a different manner. In essence, only the regrouped groundmass of fine-grained detritus composing the original snow aggregates was measured. The entire 1/16th split was examined under a stereo-microscope, and the relative abundance of marine snow was estimated with the aid of standardized graphics displaying the percentage coverage of a circle by dark particles (Terry and Chilingar, 1955). Using the surface area of the microscope slide as the area of the circle, the proportion covered by marine snow aggregates was then converted to absolute units (mm^2).

The graphics were originally designed for sedimentology studies, and we therefore used them as well to determine the surface area of the mineral grain particles. To evaluate the experimental error using this slightly subjective technique, we performed blind tests on 12 different samples, each analyzed 6 times. The mean variation was approximately 24%, with the lowest percentages corresponding to the greatest abundances (table 1). The relative abundance of each class of particles was determined by comparing its surface area with that of the sum of all the particles in the slide.

2. 3 Results

2. 3. 1 Vertical fluxes and organic matter content of the sedimenting particulate matter

Tables 2 and 3 list the total mass flux, carbon and nitrogen concentrations, and their corresponding vertical fluxes, for each deployment of the free-drifting traps. Comments also are included to indicate the degree of confidence we have in the utility of the respective flux estimates. The large traps intercepted between 40 and 500 mg dry

Table 1. Reproduceability using the percentage-coverage diagram (Terry and Chilingar1955).

		Porcent of the surface occupied by marine snow								
		Blind test								
Sample	Date	1	2	3	4	5	6	Mean	Std. Dev.	C.V. %
St 1 Large	Apr12/94	15	18	20	18	18	20	18,2	1,8	10,1
St 1 small	Apr/12/94	1	2	1	1	2	1	1,3	0,5	38,7
St 1 small	Jul/11/93	3	2	5	3	5	3	3,5	1,2	35,0
St 2 Large	Jun/22/94	20	18	22	20	20	20	20,0	1,3	6,3
St 2b small	Apr/15/94	3	2	3	1	3	2	2,3	0,8	35,0
St 3 Large	Jun/25/94	2	2	3	3	2	2	2,3	0,5	22,1
St 4 Large	Apr/17/94	10	13	12	10	10	15	11,7	2,1	17,7
St 5 Large	Nov/30/93	5	3	5	5	5	3	4,3	1,0	23,8
St 5 small	Nov/30/93	7	10	7	10	7	7	8,0	1,5	19,4
St 6 Large	May/29/93	7	5	5	7	10	7	6,8	1,8	26,9
St 6 small	May/29/93	3	2	3	2	3	3	2,7	0,5	19,4
St S Large	Jun/28/94	1	2	2	1	2	1	1,5	0,5	36,5
								Average c.v. =		24,2

weight of settling material during the one-day deployments, resulting in a range of total mass fluxes of 80 to 1000 mg/m2/d. The small traps ranged from about 500 to 1500 mg/m2/d, which, in most cases (most particularly during the earlier JGOFS cruises), were notably larger than the fluxes measured with the big traps on the same date. This is attributed to the very small mass (20-50 mg) of particles actually intercepted during 24 h over the 0.03 m^2 total collecting surface of the small trap, awkwardness in manipulating the long cylinders when recovering the sample, unperfected filtration techniques, and possible contamination by plastic or terrigenous debris (note the occasionally very high C/N ratios). The differences between traps at 50 and 150 m depth were much less important during later cruises, when inter-comparisons between traps tethered at the same

Table 2. Summary of drifting sediment trap fluxes

Cruise	Date	Station	Trap	Total mass flux ($mg/m^2/d$)	Stnd. dev'n ($\pm$ mg/m2/d)	Stnd. dev'n ($\pm$ %) mean	(n =)	Quality of estimate
5	6/3/93	1	Small	752	205	27	2	Weak
5	6/3/93	1	Big	77	24	31	3	Good
6	7/11/93	1	Small	915	539	59	5	Good
6	7/11/93	1	Big	375	115	31	3	Good
7	12/1/93	1	Small	755	364	48	6	Weak
7	12/1/93	1	Big	312	31	10	6	weak
8	4/12/94	1	Small	1041	249	24	7	Good
8	4/12/94	1	Big	874	134	16	7	Good
9	6/20/94	1	Small	984	131	13	6	Good
9	6/20/94	1	Big	792	182	23	5	Very good
8	4/14/94	2	Small	1072	254	24	7	OK
8	4/15/94	2b	Small	1140	167	15	7	OK
9	6/22/94	2	Small	412	57	14	6	Good
9	6/22/94	2	Big	677	96	14	6	Very good
9	6/25/94	3	Big	87	17	20	6	Very good
5	6/1/93	4	Small	1198	478	40	2	Weak
6	7/16/93	4	Small	1037	343	33	3	Weak
7	11/28/93	4	Small	647	135	21	6	Good
8	4/17/94	4	Small	990	250	25	7	Good
8	4/17/94	4	Big	550	68	12	7	Very good
9	6/16/94	4	Small	489	18	4	6	Good
7	11/30/93	5	Small	1536	272	18	6	Good
7	11/30/93	5	Big	182	72	40	6	Dubious
8	4/19/94	5	Small	713	192	27	7	Good
8	4/19/94	5	Big	166	36	22	7	Very good
9	6/18/94	5	Small	1644	196	12	7	Good
9	6/18/94	5	Big	1089	150	19	5	Very good
5	5/29/93	6	Small	1226	670	55	2	Weak
5	5/29/93	6	Big	207	62	30	3	Good
6	7/14/93	6	Small	633	341	54	3	Weak
6	7/14/93	6	Big	193	90	47	5	Good
9	6/28/94	S	Big	89	80	89	6	Dubious

Table 3. Organic matter components of the vertical flux.

Cruise	Date	Station	Trap	Carbon % by wt.	Nitrogen % by wt.	C/N ratio	Carbon flux mg C/m^2/d	Nitrogen flux mg N/m^2/d
5	6/3/93	1	Small	22.2	2.79	8.0	167	21.0
5	6/3/93	1	Big	25.5	4.44	5.7	20	3.4
6	7/11/93	1	Small	28.1	1.41	20.0	257	12.9
6	7/11/93	1	Big	12.7	1.51	8.4	48	5.7
7	12/1/93	1	Small	25.8	1.36	18.9	195	10.3
7	12/1/93	1	Big	5.7	0.49	11.5	18	1.5
8	4/12/94	1	Small	14.2	1.20	11.8	147	12.5
8	4/12/94	1	Big	7.7	0.60	12.8	67	5.3
9	6/20/94	1	Small	15.5	1.14	13.6	153	11.2
9	6/20/94	1	Big	9.2	0.92	10.1	73	7.3
8	4/14/94	2	Small	11.6	0.92	12.6	124	9.9
8	4/15/94	2b	Small	10.8	0.80	13.5	123	9.1
9	6/22/94	2	Small	21.3	1.71	12.5	88	7.0
9	6/22/94	2	Big	11.6	1.23	9.4	78	8.3
9	6/25/94	3	Big	18.6	1.72	10.8	16	1.5
5	6/1/93	4	Small	25.2	3.52	7.2	302	42.2
6	7/16/93	4	Small	21.3	2.75	7.7	220	28.5
7	11/28/93	4	Small	14.1	0.99	14.2	91	6.4
8	4/17/94	4	Small	12.1	0.75	16.1	120	7.4
8	4/17/94	4	Big	6.5	0.72	9.0	36	4.0
9	6/16/94	4	Small	25.0	1.26	19.8	122	6.2
7	11/30/93	5	Small	9.7	0.90	10.8	149	13.8
7	11/30/93	5	Big	12.6	1.36	9.3	23	2.5
8	4/19/94	5	Small	11.6	1.04	11.2	83	7.4
8	4/19/94	5	Big	6.3	0.71	8.8	10	1.2
9	6/18/94	5	Small	11.2	1.04	10.8	184	17.0
9	6/18/94	5	Big	11.2	1.20	9.4	122	13.0
5	5/29/93	6	Small	6.4	0.35	18.2	78	4.3
5	5/29/93	6	Big	16.3	2.70	6.0	34	5.6
6	7/14/93	6	Small	22.2	2.16	10.3	140	13.7
6	7/14/93	6	Big	11.8	1.16	10.1	23	2.2
9	6/28/94	S	Big	5.3	0.36	14.8	5	0.3

depth were also made. However, a test of the effect of the collecting area of the large and small cylinders, using cylinders from the small trap mounted on the frame of the large trap (see fig. 3) showed that the small cylinders almost always gave higher measurements of the total mass flux, whether the cylinders were on the small trap frame with the two traps at the same depth, or when the small cylinder was on the large trap frame. In other words, the small cylinders trapped more mass per unit area than the large traps. Fluxes of planktonic organisms and other biogenic particles were similarly affected by the type of trap used. The composition of the sedimenting material (carbon and nitrogen contents in wt %) is thus known with greater precision than the corresponding fluxes, because of the uncertainties associated with the values of the total mass flux.

The results from the two successful time-series traps are shown in figures 4 and 5. It is notable that the total flux and the carbon fluxes in the Anticosti Gyre remained elevated throughout the fall and winter. The carbon contents are not as high as during the ice-free months, but the C/N ratios remain low, suggesting that there is still not much dilution with terrigenous detritus, even in winter. Although there is some indication of higher carbon contents in very early spring, the trap did not remain in place long enough to detect the spring bloom, anticipated for April. The individual cups contained between 200 and 1200 mg dry weight of collected material, allowing for relatively accurate flux measurements. The Emerald Basin trap (fig. 5) apparently sampled only the tail-end of the spring bloom. The remainder of the summer, although carbon contents are still high, typical of pelagic suspended particulate matter, the fluxes are very low. Only the first cup contained as much as 200 mg of material; the others contained much less. Unfortunately, no other trap data are available for this site.

2. 3. 2 Microscopic characterization of the trap material

During the “rest” periods on deck, it was often possible to observe fluffy aggregates several millimeters in diameter slowly settling through the transparent tubes at the base of the cones of the large trap. On-board binocular scope examinations of the fresh Pasteur

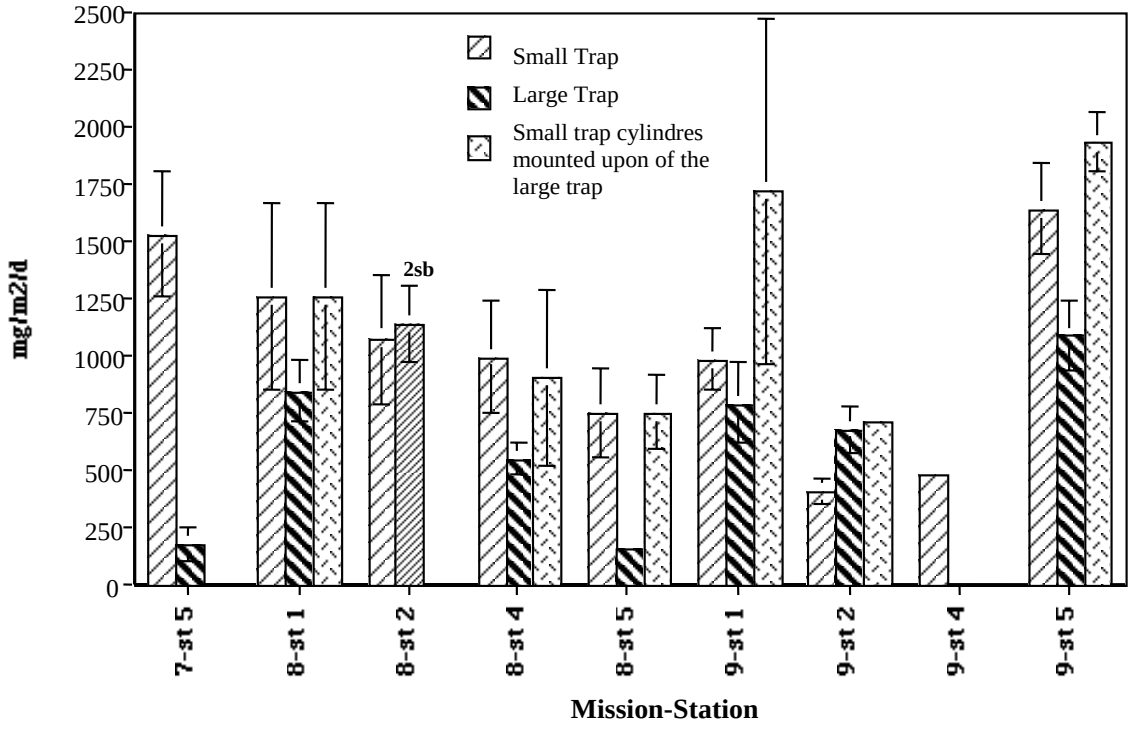

Figure 3. Comparison of total mass fluxes obtained from small traps, large traps and from small-trap cylinders mounted upon the frame of the large trap. Note: 2sb does not refer to a large trap, but to a second small trap deployed at the same St.2 site one day after the first.

pipette samples revealed many integral particles: marine snow aggregates and fecal pellets, as well as whole zooplankton (fig. 6a and b). Once the material was fixed, however, and subjected to the various steps of sample preparation, the marine snow was mostly disaggregated and the fecal pellets were also in fragments (Fig. 6c), and the fragile structures of the phytoplankton became included in the marine snow.

Most of the sediment trap samples were almost free of organisms larger than 1 mm. Of the 12 samples which had measurable numbers of “swimmers” retained on the 1 mm screen (table 4), 8 were from the 9 traps of June 1994, 2 from the 8 traps of April

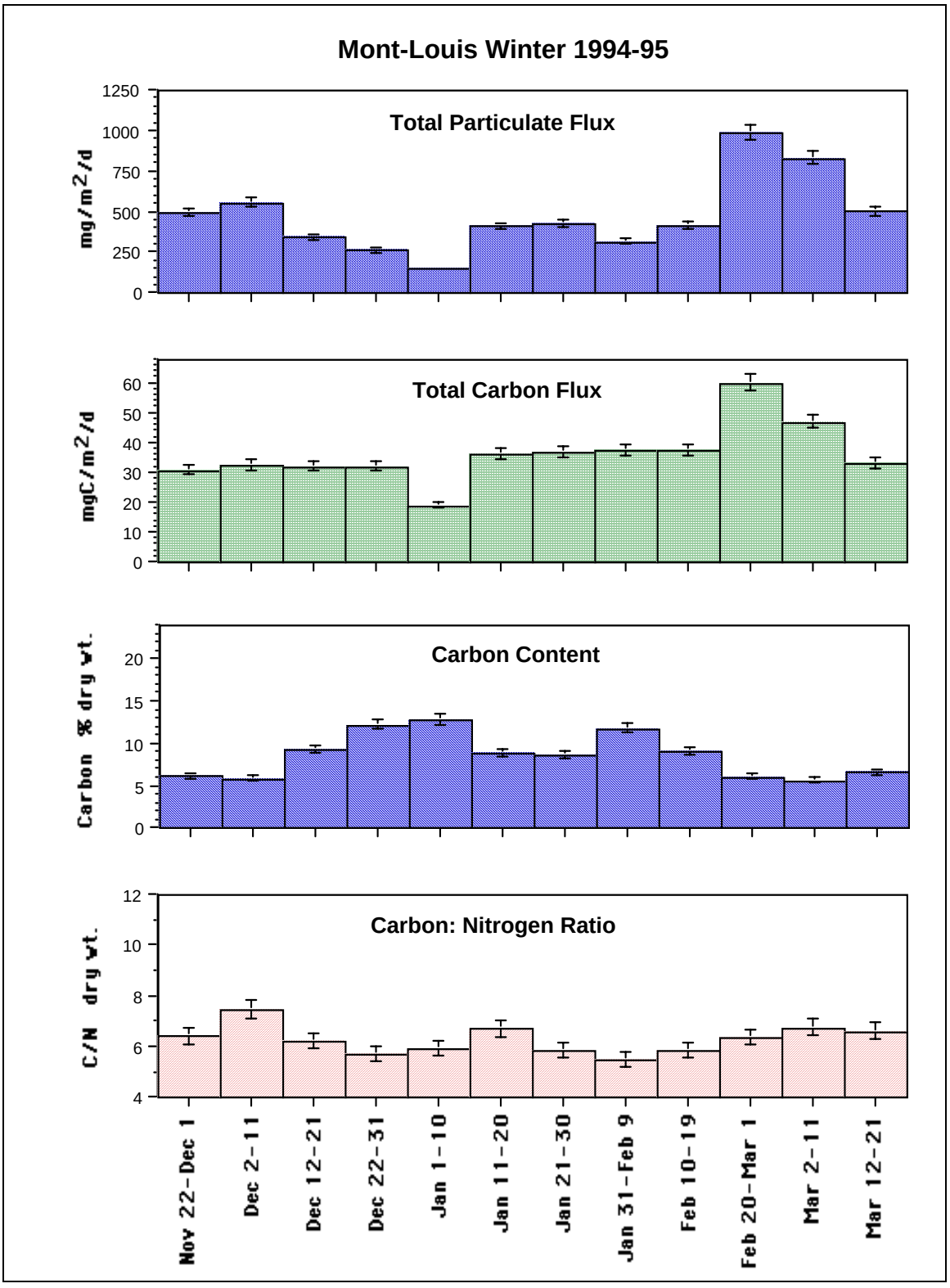

Figure 4. Fluxes of total mass and carbon, carbon content (% dry wt.) and the C/N ratio (dry wt.) for the time-series Technicap trap deployed at St. 1 Anticosti Gyre for 5 months between November 1994 and March 1995.

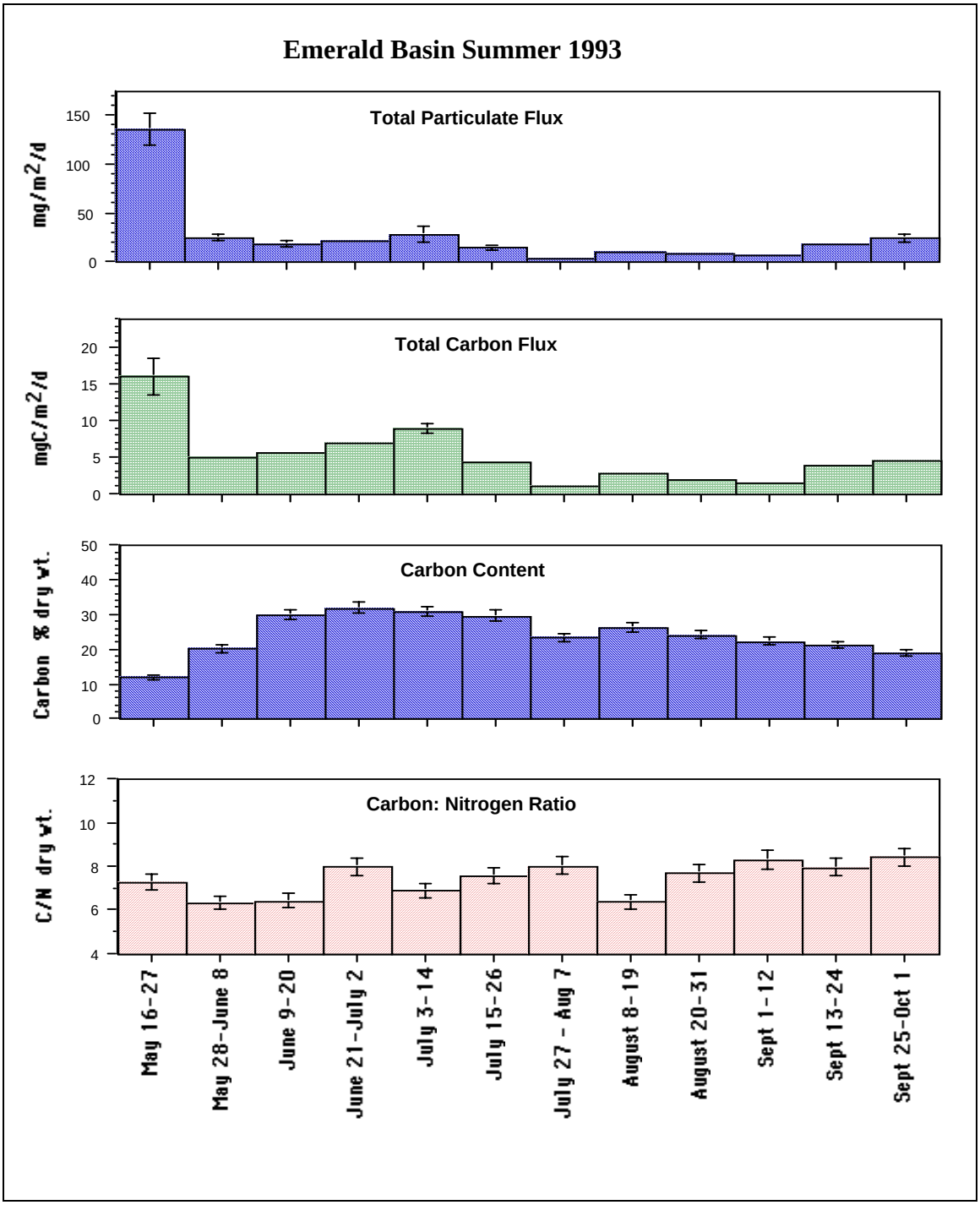

Figure 5. Fluxes of total mass and carbon, carbon content (% dry wt.) and the C/N ratio (dry wt.) for the time-series Technicap trap deployed in Emerald Basin for 5 months from mid-May through September 1993. Note the very low fluxes (for all samples save the first one) and the much higher carbon contents at this site compared to the Anticosti Gyre.

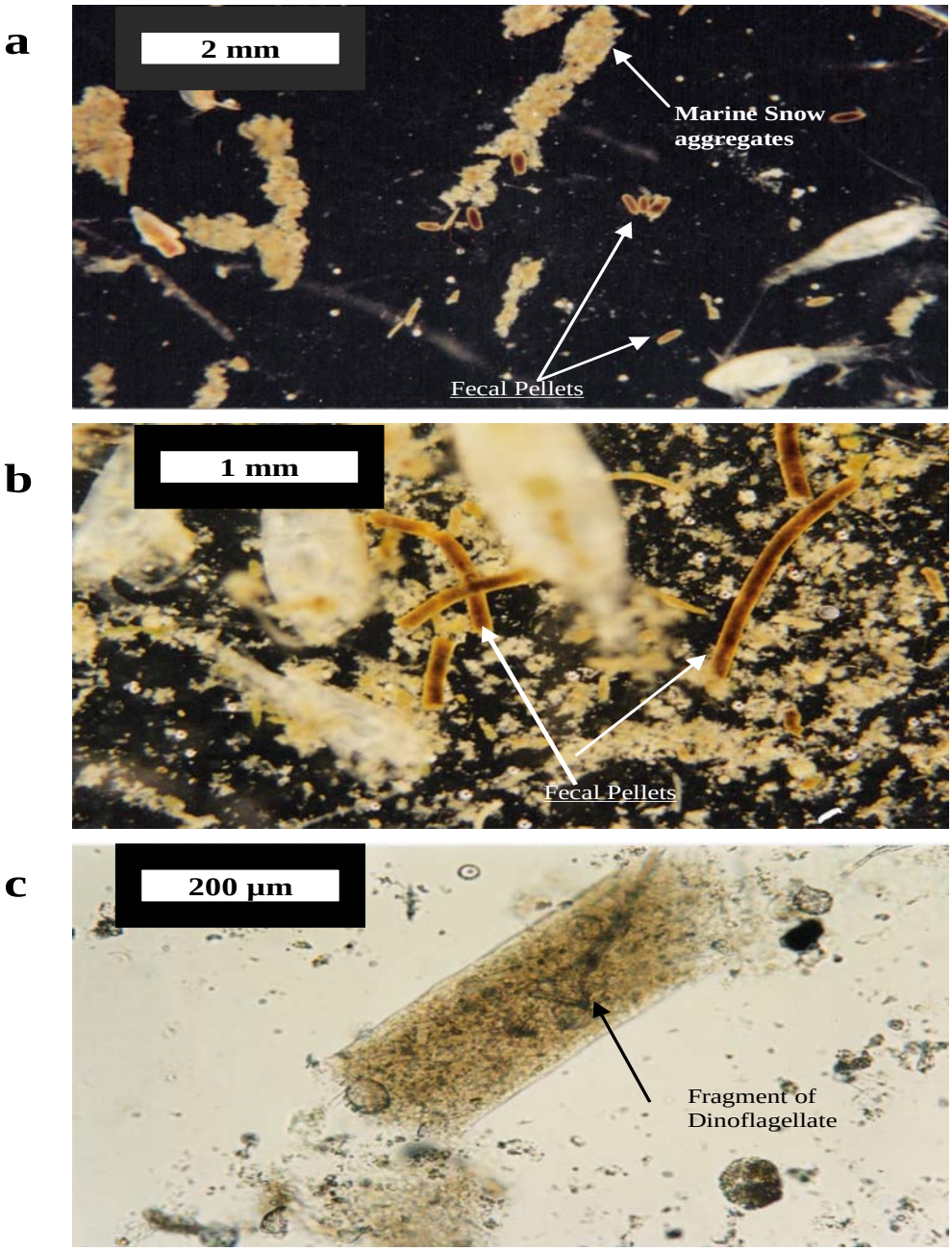

Figure 6. Photographs of sediment trap material: (a) and (b) Examples of freshly collected material. Note the large, separate patches of marine snow, intact faecal pellets and copepod swimmers. (c) After sample treatment the marine snow is mostly dispersed and faecal pellets can be fragmented. Bar represents 2 mm in (a), 1 mm in (b); and 200 µm in (c).

Table 4. Numbers of the various organisms in the >1mm fraction ("swimmers").

Cruise	JGOFS - 6				JGOFS -8				JGOFS -9															
	St. 1 - Large		St. 6 - Large		St. 1 - Large		St. 4 - Large		St. 1 - Large		St. 1 - Large		St. 2 - Large		St. 3 - Large		St. 4 - small		St. 5 - Large		St. 5 - small		St. S - Large	
Organism	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total	#	% of total
Copepods	580	99,0	611	99,5	1041	97,4	935	100	3920	98,4	92	95,8	320	97,6	343	86,0	128	96,2	832	97,5	50	84,8	67	66,3
Chaetognaths			2	0,3	1	0,1			1	0,0					2	0,5	3	2,3	2	0,2	4	6,8	4	4,0
Amphipods	6	1,0	1	0,2	12	1,1			28	0,7			4	1,2	7	1,8	1	0,8	8	0,9	1	1,7	1	1,0
Ostracods					2	0,2			8	0,2			1	0,3	29	7,3	1	0,8	4	0,5	1	1,7		
Cnidaria					1	0,1																	1	1,0
Cladocera					7	0,7			12	0,3					7	1,8							1	1,0
Euphausiids																			1	0,1				
Copepods egg-sacks					3	0,3			2	0,1			2	0,6	1	0,3					2	3,4		
Fish egg									3	0,1									6	0,7			1	1,0
Polychaetes									1	0,0														
Cirriped larvae															6	1,5								
Decapods																								
Pteropods																							26	25,7
Crustacean frag.																					1	1,7		
Ctenophores									2	0,1	1	1,0												
Hydrozoa					1	0,1																		
Crab larvae									7	0,2	3	3,1	1	0,3	1	0,3								
Decapodos cf.															3	0,8								
Total	586	100	614	100	1068	100	935	100	3984	100	96	100	328	100	399	100	133	100	853	100	59	100	101	100

Large: Large trap
Small: Small trap

1994 and 2 from the 5 traps of July 1993. Copepods were by far the dominant organisms encountered, representing at least 85% of the individual swimmers identified in Gulf samples (60% in the Slope trap). Others included: amphipods, ostracods, pteropods (unshelled *Limacina* spp. were found in some abundance at the continental slope site, St. S), cladocerans, chaetognaths, polychaetes, ctenophores, as well as much smaller organisms such as cirriped and crab larvae. A small number of copepod egg sacks also were identified, some still attached to copepod bodies. The material that passed the 1 mm sieve was used for the detailed microscopic analysis. Six major types of particles were identified: fecal material, phytoplankton, zooplankton, marine snow, mineral grains and pollen.

Marine snow: Various forms of mucous-bound aggregate particles have been reported from near-surface waters, where collection of individual marine snow aggregates by divers is possible (Alldredge and Silver, 1988). However, once such aggregates have mingled with the rest of the material at the base of the sediment trap collecting tube, their original dimensions and some characteristics are lost. Freshly collected material still showed large aggregates (fig. 6). After much dispersal and partial reaggregation during sample preparation, marine snow under the inverted scope was identified as a groundmass of both small (dispersed) and large (probably re-aggregated) semi-transparent fluff to which adhered a heterogeneous mix of smaller detritus, such as: individual frustules and chains of diatoms; fragile organelles such as setae of the diatom of genus *Chaetoceros* and terminal processes of genus *Rhizosolenia,* mucus exudations of diatoms, crustaceans and appendicularians, pollen grains and fine mineral particles. It is impossible to tell whether some of the fecal pellets, phytoplankton and zooplankton, counted separately, had originally been incorporated within larger marine snow aggregates.

Fecal pellets: These represented the largest, heaviest particles sampled. In the fixed samples, they were generally darker and showed much evidence of having been broken during sample manipulation. They have been separated in this study into four particle subclasses, according to their form and consistency: compact rods (fig. 7a); loose rods (fig. 7b); compact oval pellets (fig. 7c) and small loose rods (fig. 7d). Compact rods

have the form of elongated cylinders. They are quite dense with a dark brown

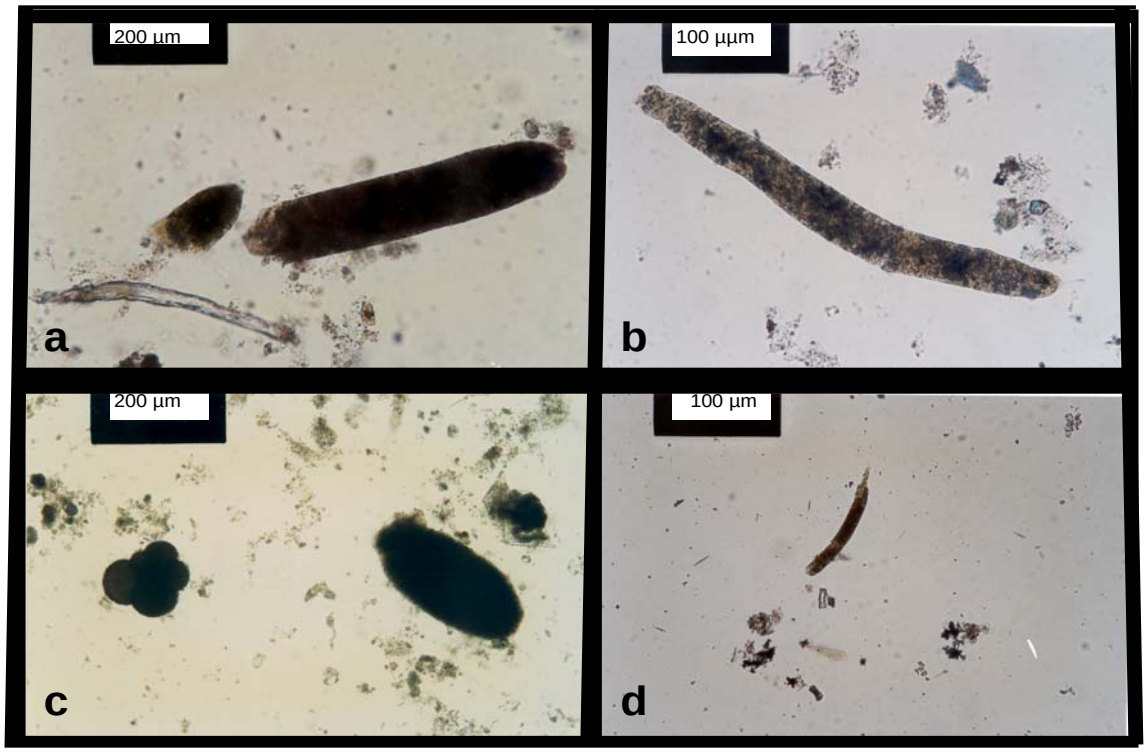

Figure 7. Inverted microscope photos of the various types of fecal pellets noted in this study: (a) compact rod, bar = 200 µm; (b) loose rod bar = 100 µm; (c) compact oval, bar = 200 µm and (d) small loose rod, bar = 100 µm.

coloration. They are often seen as solid fragments (mean length = 195 ± 87 µm, mean diameter = 79 ± 21 µm), still sheathed in a peritrophic membrane. The internal matrix of this type of rod was generally not discernible under the microscope, except when full of pollen grains.

Loose rods, although also possessing peritrophic membranes, are not as dense as compact rods and are generally more fragmented. They average about 169 ± 71 µm in length and 73 ± 22 µm in diameter. The internal contents are usually discernible and can sometimes be identified, particularly if they contain pollen or armored dinoflagellates which may easily break the membrane.

Small loose rods are the least abundant and smallest (81± 15 µm length and 35 ± 7 µm diameter) of the fecal pellets found in the trap samples. They are generally cylindrical but also may be fusiform, when the extremities appear to be empty. Although

clearly delimited by a membrane and not strongly compacted, the internal contents are opaque and not identifiable.

Oval pellets, composed of more strongly compacted material, are never observed in fragmented form. Their diameter averages 90 ± 18 µm with a mean length of 153 ± 41 µm. Generally the darkest colored and opaque of all, the internal contents are not discernible beneath their membrane.

Phytoplankton: The taxonomic groups analyzed consist predominantly of microphytoplankton (20 - 200 µm; Lalli and Parsons, 1993). The subclasses identified were: centric diatoms, pennate diatoms, dinoflagellates, silicoflagellates and "others". The latter includes the smallest microphytoplankton and some nanophytoplankton (2 - 20 µm). A total of 10 genera of centric diatoms were identified, the most abundant being chain-forming genera (*Thalassiosira* spp, and *Chaetoceros* spp.). Most of the centric diatoms retained at least 50% of their original pigments. Long-chained forms displayed the most intact chloroplasts. Short-chains and individual frustules were more common, likely due to breakup during sample manipulation. In such cells, the chloroplasts were reduced or absent. Rare, small aggregates of centric diatoms (*Thalassiosira*) were observed in the samples of June 1994. These were bound together in a semi-transparent matrix in the interior of small irregular-shaped conglomerates.

Sixteen genera of pennate diatoms were identified, among which only two were chain forming (*Fragilariopsis* and *Thalassionema*), and were rich in chloroplasts. Save for some species of *Nitzschia* spp., the isolated frustules did not conserve their chloroplasts. The most common individual pennate genera were *Navicula*, *Nitzschia*, *Gyrosigm*a, *Amphora*, and *Grammatophora*. Five genera of dinoflagellates were identified, always as isolated cells. *Protoperidinium*, *Dinophysis* and *Ceratium* were the most prevalent. No resting cells or cysts were observed.

Zooplankton: The most common zooplankters in the < 1 mm trap material were tintinnid protozoans. *Parafavella* (fig. 8d), *Tintinnopsis* (fig. 8e) and *Codonella* were common genera, often observed with their external test filled. However, it was not

possible to determine if this was protoplasmic material or trapped detritus. *Stenosemella*

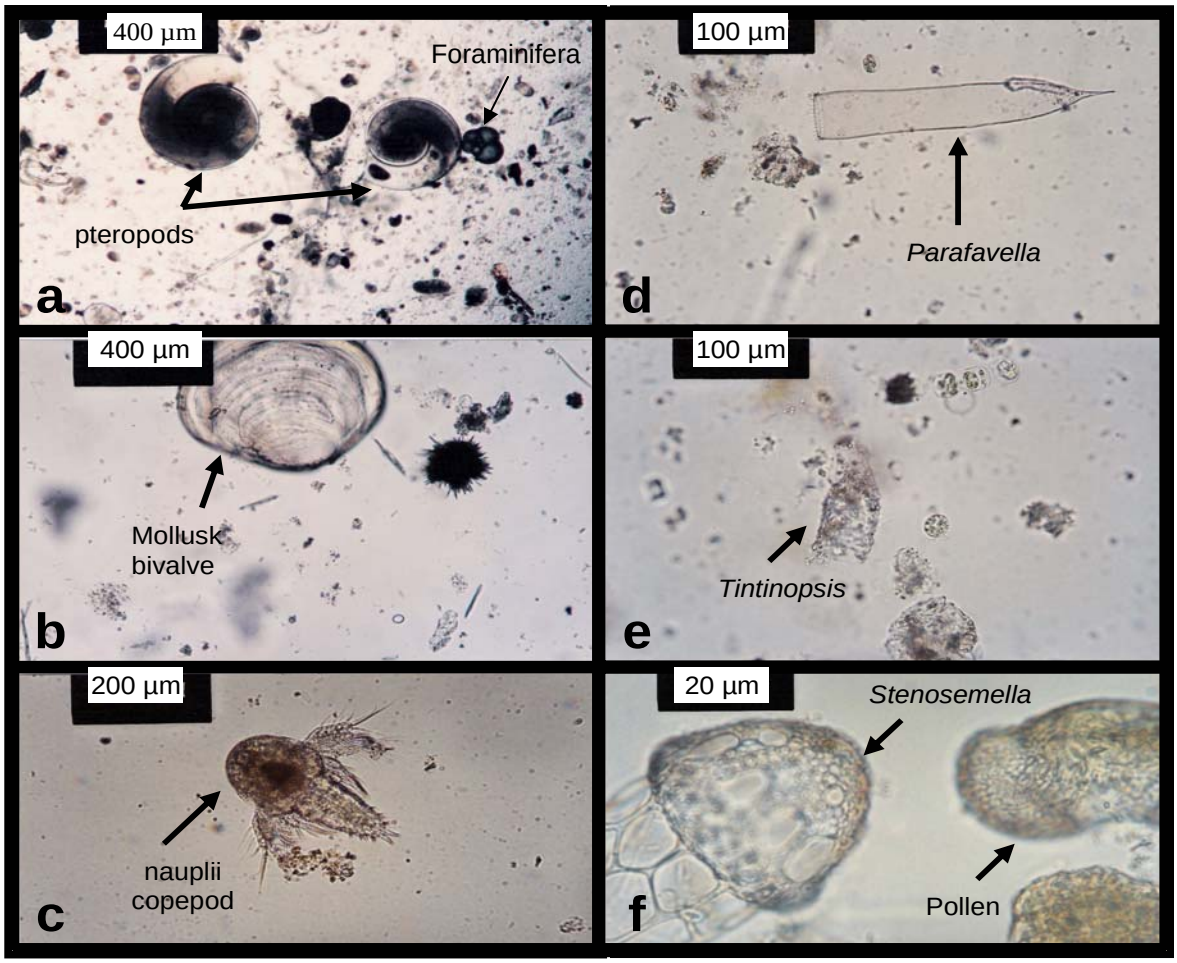

Figure 8. Examples of zooplankton particles: (a) and (b) molluskan microzooplankton, bar = 400 µm; (c) crustacean nauplii (copepod), bar = 200 µm; common tintinnid lorica protozoans: (d) *Parafavella*, bar = 100 µm and (e) *Tintinnopsis*, bar = 100 µm; rare (f) *Stenosemella*, bar = 20 µm and pollen (not zooplankton particle).

(fig. 8f) was a rare genus in the traps. Other microzooplankton encountered was: larval forms of mollusks (figs. 8b) and nauplii crustaceans copepods, (fig. 8c); echinoderms, foraminifera (fig. 8a). Larger, soft-structured organisms, such as siphonophors, and others such as pteropods (fig. 8a), polychaetes and fragments of larger organisms (e.g., calanoid copepods such as *Euchaeta* sp.) also were recorded as zooplankton. Fish and crustacean eggs, juvenile stages of copepods, and smaller copepods such as *Oithona* sp. also were observed.

Mineral grains: Sand- and silt-sized grains of individual minerals (e.g., quartz,

mica) and fragments of rocks were generally rare in the samples, although clay-sized particles were probably hidden within the marine snow and fecal pellets. In June 1994, a few traps received measurable quantities of these grains, perhaps indicative of strong winds in the Gulf in the days immediately before the cruise.

Pollen: These particles of terrestrial origin also were encountered in the traps. When they were abundant (June 1994) they gave a yellow coloration to the samples. Only one type of pollen was identified, that of a species of fir common to the coast of eastern Canada: *Abies balsamea*. It displays a spherical form with globular protuberances and a reticulated surface.

2. 3. 3 Abundance of the different classes of particles: numerical

Centric and pennate diatoms average 64.3% of the total number of particles in the traps. The fluxes ranged over two orders of magnitude among seasons and stations, (with highest fluxes in April and June 1994). The results are shown for each type of trap in figure 9 for easier comparison of the importance of the various contributing particles. The phytoplanktons are indicated as cell numbers, corrected to take into account the presence of chained forms for some species. The fecal matter counts include broken pellets, and are thus somewhat high. Zooplankton includes individual organisms, tintinnid structures, eggs and fragments of larger organisms. Considering their breakup during sample preparation, we have not found a satisfactory way to enumerate marine snow as particle numbers.

In spite of the large difference in the range of absolute numeric fluxes (table 5), the proportional contribution of the different particle types to the total flux is very similar for the large and the small traps. Thus, total phytoplankton cells, fecal pellets and zooplankton particles account for a mean of 61, 24 and 14%, respectively, of the total numeric flux in the small traps and 67, 18 and 12%, respectively, in the large traps. The two traps collect, albeit with different efficiencies, essentially the same mix of particles. In detail, however, there is some tendency for the phytoplankton/fecal pellet ratio to be lower in the small traps at many stations, again suggesting a greater sampling efficiency for large, heavy particles in the small cylinders.

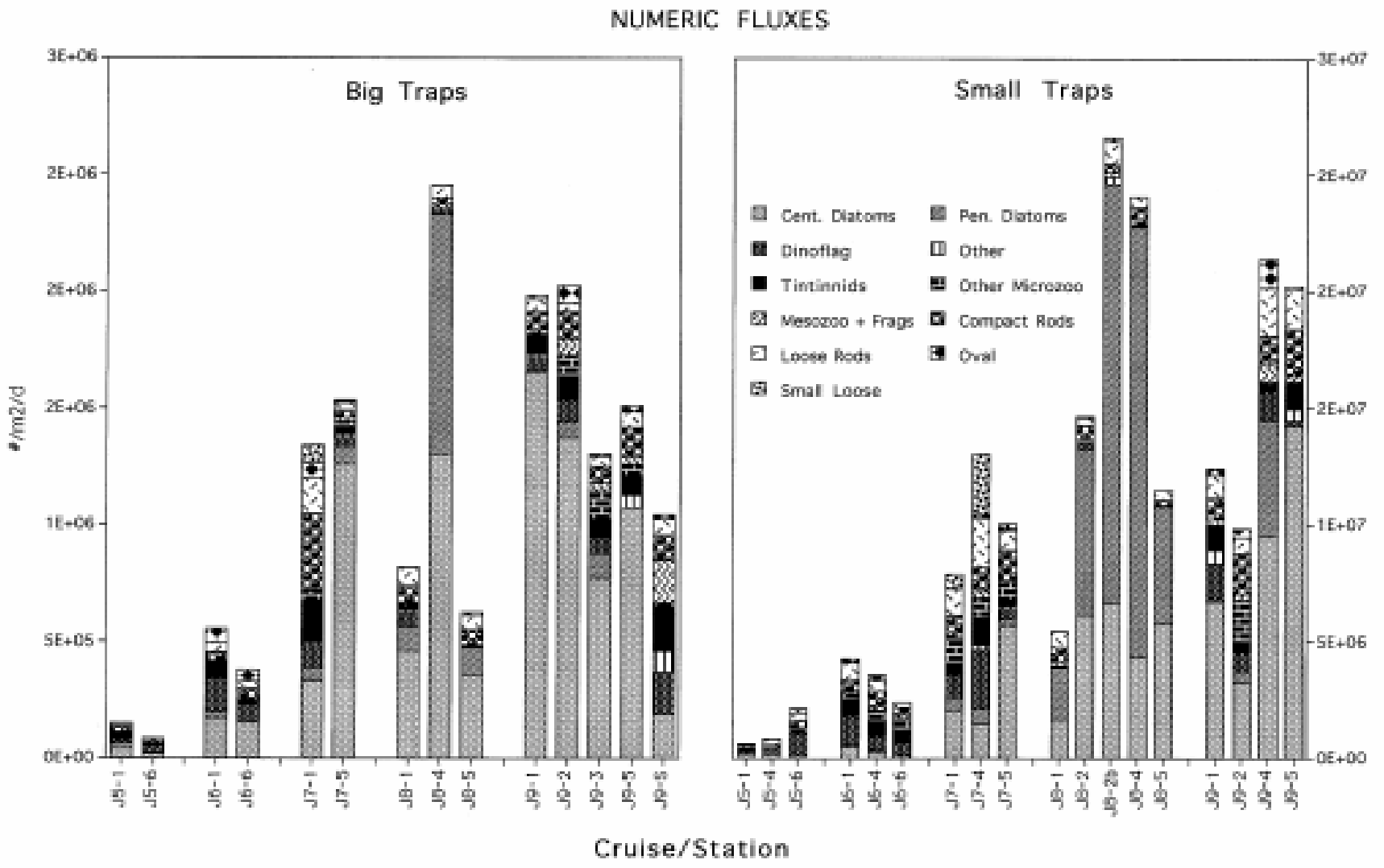

Figure 9. Contribution to total numeric flux of different particles types in the large and small traps.

Tabla 5. Numeric fluxes from various regions of the world ocean

Area	Phytoplankton # m^{-2} d^{-1}	Fecal pellets # m^{-2} d^{-1}	Trap depth (m)	Observations	Reference
Gulf of St-Lawrence					
Range	3.1E+05 - 2.5E+07	1.3E+05 - 5.9E+06	Small 50	Deep inland sea	This study
Mean	7.8E+06	1.90E+06			
Range	5.0E+04 - 9.9E+06	1.8E+04 - 2.4E+06	Large 50, 150		
Mean	1.5E+06	3.20E+05			
Bjornafjorden	1.6E+06	nd	50	Fjord	González *et al. (* 1994b)
	8.10E+06	nd	100		
Dabob Bay	nd	4.05E+06	50	Deep inland sea	Buck and Newton (1995)
Nova Scotia coast	0.2-2.5 E+07	1E+04 - 1E+06		Bedford Basin	Hargrave and Taguchi (1978)
California coast	0.4 - 4.7 E+08	2E+02 - 6E+04	50-225	Upwelling zone	Silver and Gowing (1991)
Northern Adriatic Sea	nd	0- 216	25-35	Shallow coastal	Puskaric *et al* . (1992)
SE Hudson Bay	nd	1 - 3.5 E04	45	Coastal Ice	Tremblay *et al.* (1989)
Scotia & Weddell Seas	nd	170- 850	50-150	Ice Margin	Cadeé *et al.* (1992)
Continental margin	1,00E+09	nd	-	during a bloom	Parsons *et al.* 1984 op. cit.
					Bathmann *et al.* (1990)
E Tropical Pacific	2.6 - 7.6 E+07	2.7 - 3.5 E+03	80-700		Silver and Gowing (1991)
					Gowing and Silver (1985)
Norwegian Sea	<3 E+04	2E+05 - 1.5 E+06	1300	Continental Slope	Bathmann *et al* . (1990)
	5E+04 - 2E+05 (bloom)				
NE Pacífico St. Papa	4.6E+06 - 2.8E+07	nd	3800	Océano abierto	Takahashi *et al.* (1990)
NE Pacific Ocean	1.9 - 4.5 E+06	1E+02 - 1E+03	600	Open Ocean	Silver and Gowing (1991)
Equatorial Atlantic	5E+06-1.2 E+07 (diatoms)	nd	696 & 853	Open Ocean	Lange *et al.* (1994)
	2.5E+04 (silicoflag.)	nd		"upwelling site"	
NE Atlantic	1E+06 (diatoms)	<<1 - 2 E+03	120-324	Open Ocean	Pasow and Peinert (1993)
	2E+04 - 1E+05 (dinoflag.)				
	1E+04 (silicoflag.)				
Lingurian Sea	nd	1.06E+03 - 3.74E+04	80 -200	Mediterranean	Miquel *et al.* (1994)
NE Pacífico-Monterrey	nd	2-3E+05	35-150	Continental margin	Urrère Knauer (1981)
		0.4E+05 - 0.8E+05	500-1500		
Sargasso Sea	nd	9.51E+04	5249	Open Ocean	Honjo (1978)

Figures 10-12 show the relative contributions of the different particles comprising the measured numeric fluxes. The data from May to June, July and November-December 1993 indicate an approximately equal contribution of the different particle types. The much greater numeric fluxes in April 1994 are due almost entirely to the presence of large numbers of diatoms. Pennate forms were particularly abundant, followed by centric diatoms. In June 1994, diatoms were still abundant in the vertical flux, but centric forms were much more important than pennate forms, and there was again a significant contribution of non-phytoplankton particles. A similar association was observed for Station 5 in December 1993.

Details of the relative abundances of the various classes of fecal pellets and their diameters are presented in figure 13. Compact and loose rod-shaped forms were abundant in all size classes. Particles with diameters between 50 and 109 µm (classes B and C in fig. 13) were consistently the most abundant fecal pellets in virtually all the trap samples. Fecal pellets with diameters of 20-49 µm (class A) were much less abundant in the traps, and probably originate with smaller copepods. In particular, the November-December 1993 traps uniquely contained abundant numbers of the easily differentiated class of small loose rods. Larger fecal pellets (110-200 µm diameters) occurred sporadically, probably representing the contribution of large-sized mesozooplankton, such as euphausids, mysids and amphipods. Oval-shaped fecal pellets are particularly noticeable in samples from May, June and July.

2. 3. 4 Abundance of the different classes of particles: surface area

The numeric fluxes presented above provide a valuable characterization of the particles comprising the vertical flux, and permit comparison with other numeric studies (table 5). However, the individual particles counted vary in size between about 10 µm (individual diatom cells) and several hundred microns (zooplankton larvae and detritus), and the numbers do not necessarily reflect their true contribution in terms of the bulk (volume or mass) of the sedimenting particles. Also, marine snow could not be represented. The two-dimensional surface area, summed for each class of observed

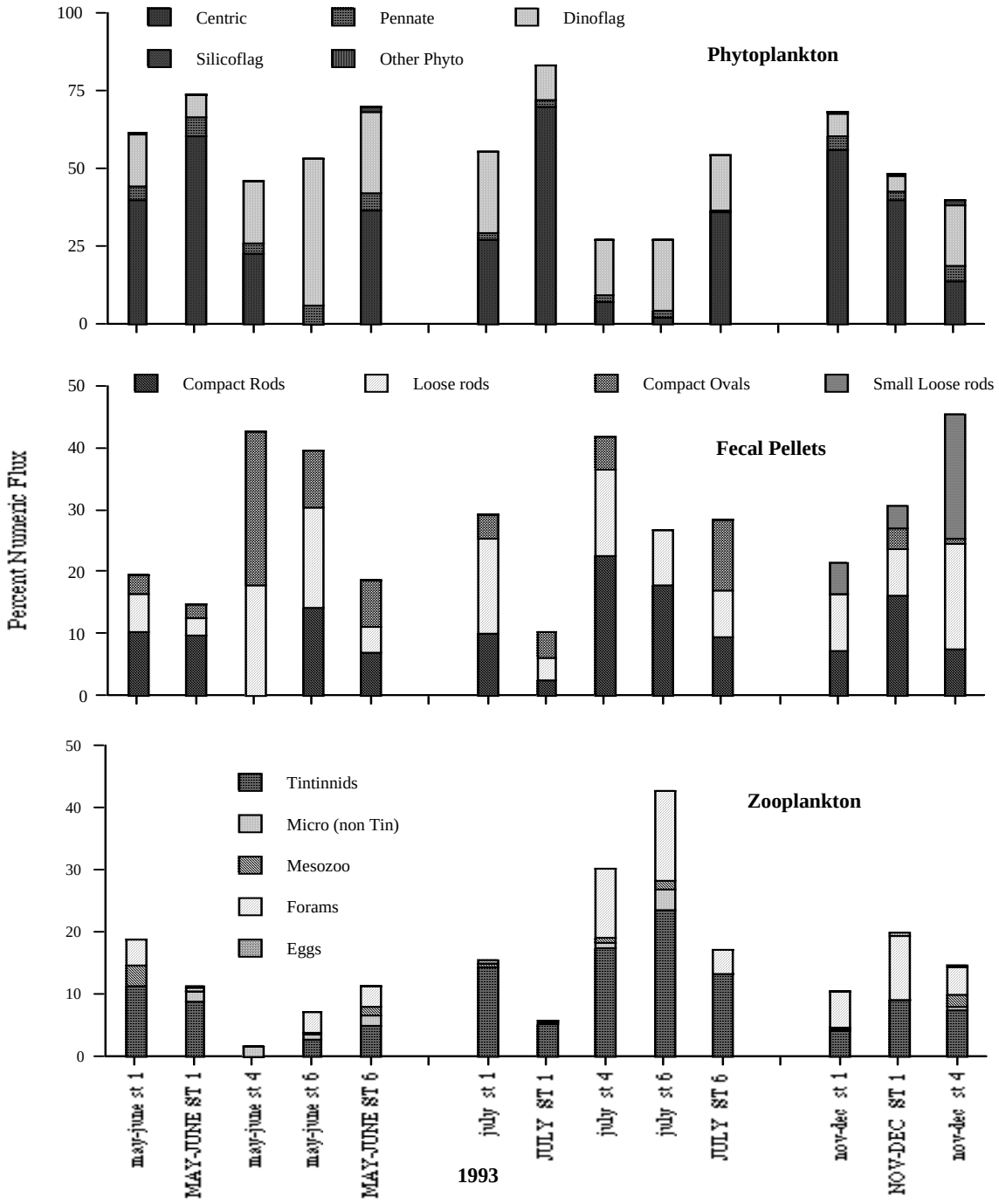

Figure 10. Non-bloom samples from 1993. Relative abundance, in terms of their numbers of the various kinds of phytoplankton, fecal pellets and zooplankton particles. Note the increase in the contribution from fecal pellets and zooplankton particles to the total numeric fluxes, and the importance of dinoflagellates to the phytoplankton fux.

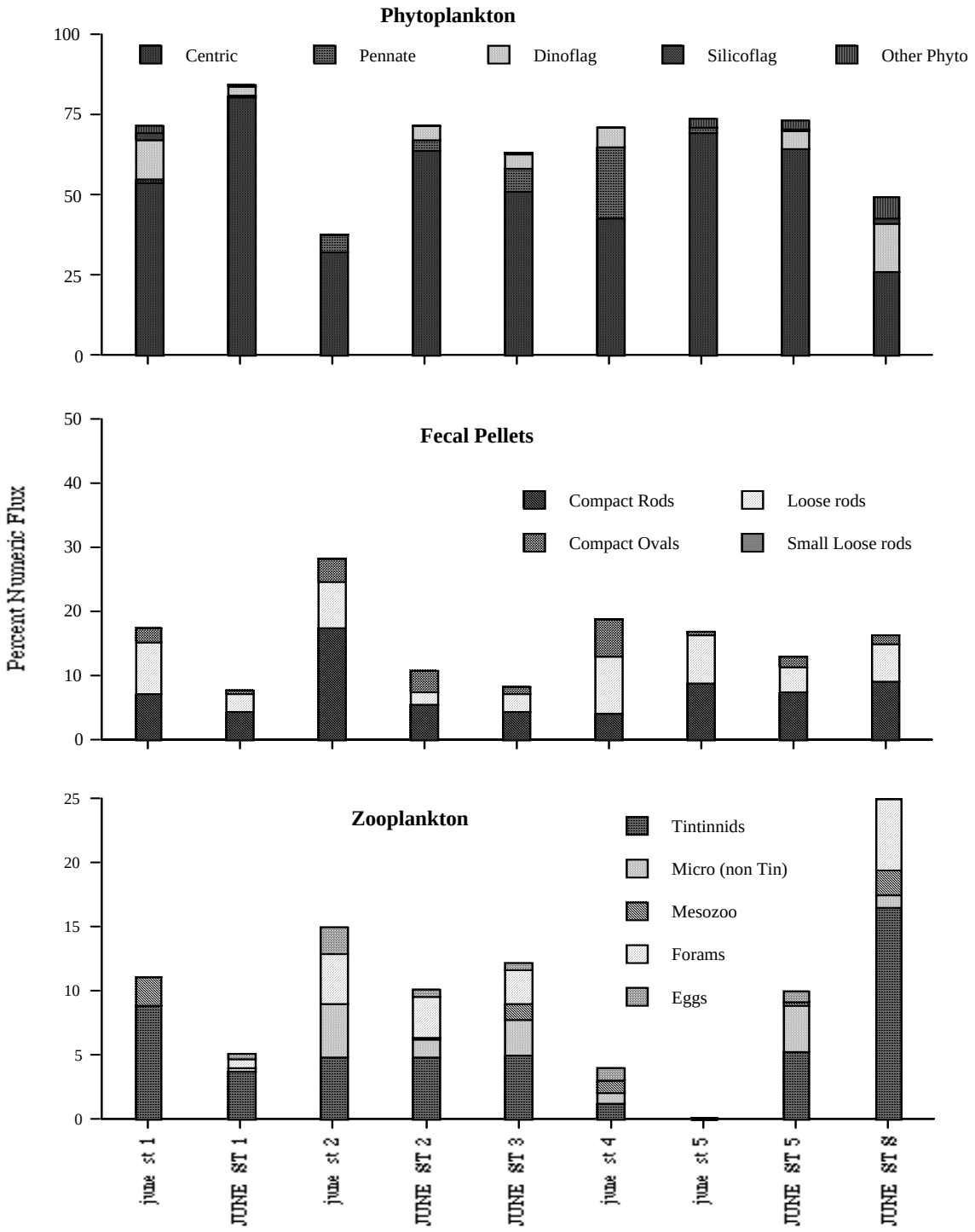

Figure 11. Spring bloom of April 1994 and late fall bloom at St. 5 in November-December 1993. Relative abundance in terms of their numbers, of the various kinds of phytoplankton, fecal pellets and zooplankton particles. Note the dominance of phytoplankton cells, including numerous pennate forms.

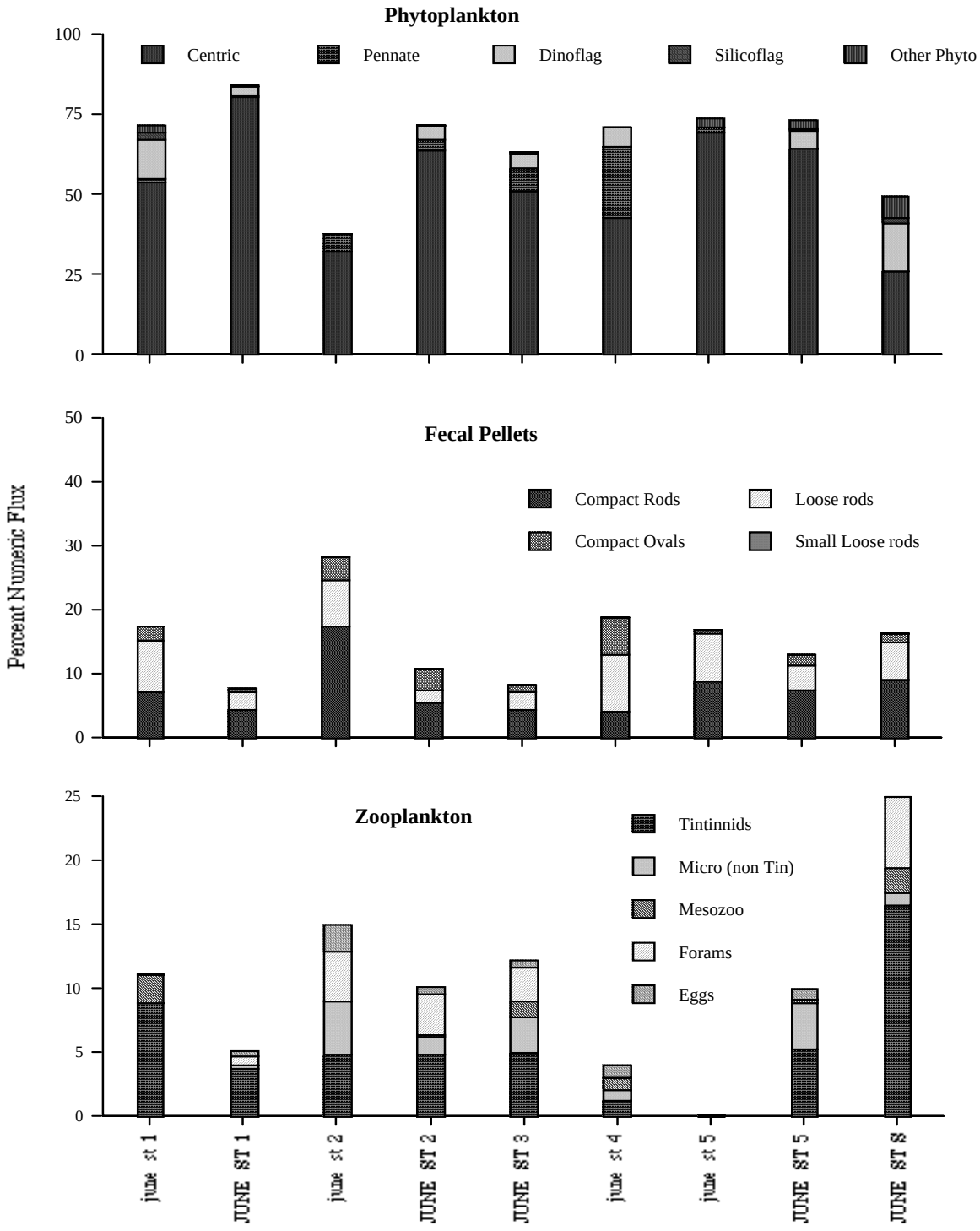

Figure 12. Post-bloom period of June 1994. Relative abundance in terms of their numbers, of the various kinds of phytoplankton fecal pellets and zooplankton particles. Note the decrease in phytoplankton contribution, particularly of pennate diatoms.

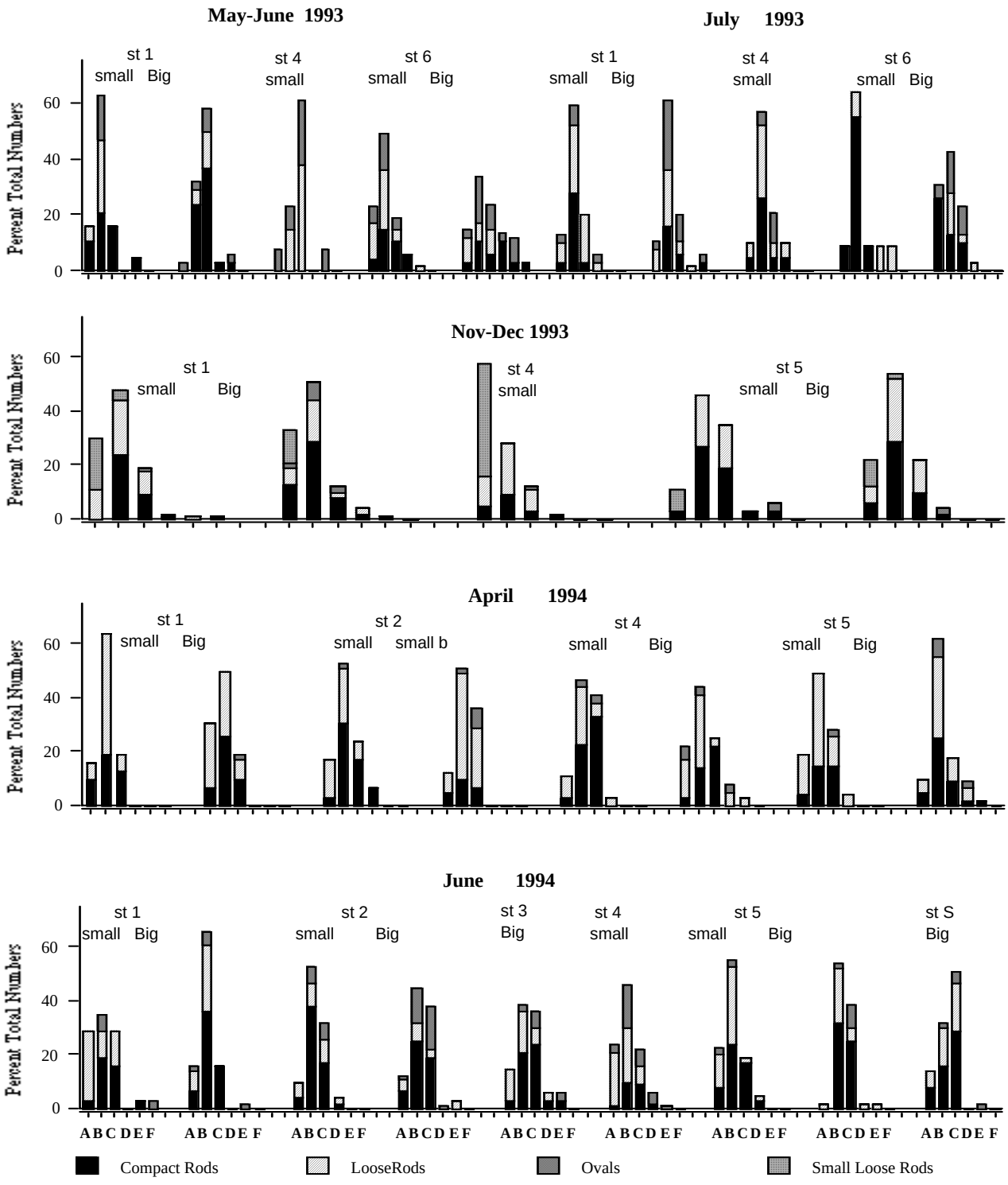

Figure 13. The contribution of the various kinds of pellet to the total numeric fecal pellet fux, as a function of pellet diameter. A=20-49 µm; B= 50-79 µm; C= 80-109 µm; D= 110-139µm; E= 140-169 µm; and F=170-199 µm. Note the strong contribution of pellets with diameters of class B and C, and the unique occurrence of small loose cylinder in November-December 1993.

particle, provides a better representation of the relative contribution to the bulk vertical flux. Relative surface areas are not affected by the additional errors involved in estimating the third dimension and the density of highly diverse, poorly known individual particles. Aspects of the conversion to volume, and thence to mass and carbon flux, will be presented elsewhere (Romero *et al*., in preparation; Roy *et al*., 2000).

In terms of 2D bulk, although phytoplanktons are still important contributors, fecal pellets are much more evident, as are zooplankton particles and marine snow. Figure 14 shows the relative abundances of each of the six principal particle classes found in the trap material for the two drifting traps for all the stations. Station 1 (st.1) was the most frequently sampled, followed by Stations (sts.) 4 and 5. The data from the other sites are only fragmentary. There is considerable variation in the proportional composition at each station and, as all particle types occur at all sites, it is difficult to group the data geographically. Phytoplankton commonly presents higher percentages in April and at St. 6. Marine snow appears to be most prevalent at St. 4, while fecal pellets are most common at the other shallow site (St. 5).

2. 3. 5 Abundance of the different classes of particles: temporal patterns

Studies of the trophic structure in the water column of the Gulf of St. Lawrence have singled out two contrasting conditions: bloom and non-bloom periods (Rivkin *et al*., 1996; Savenkoff *et al*., 1996; Savenkoff *et al*., 2000; Vézina *et al*., 2000). Although the data available are fragmentary, we also have attempted to group the sediment trap results into distinguishable time periods. For purposes of clarity, only the relative numeric abundances are presented here, although very similar groupings are evident in the relative surface area data as well. Pollen and mineral grains, being of terrestrial origin, are also excluded, so as to focus on the marine ecosystem.

Bloom period: Primary production levels greater than 1200 mg $C/m^2/d$ have only been reported for the April 1994 period (Rivkin *et al*., 1996; Savenkoff *et al*., 2000), representing the spring bloom. Measurements at other times all yielded rates less than

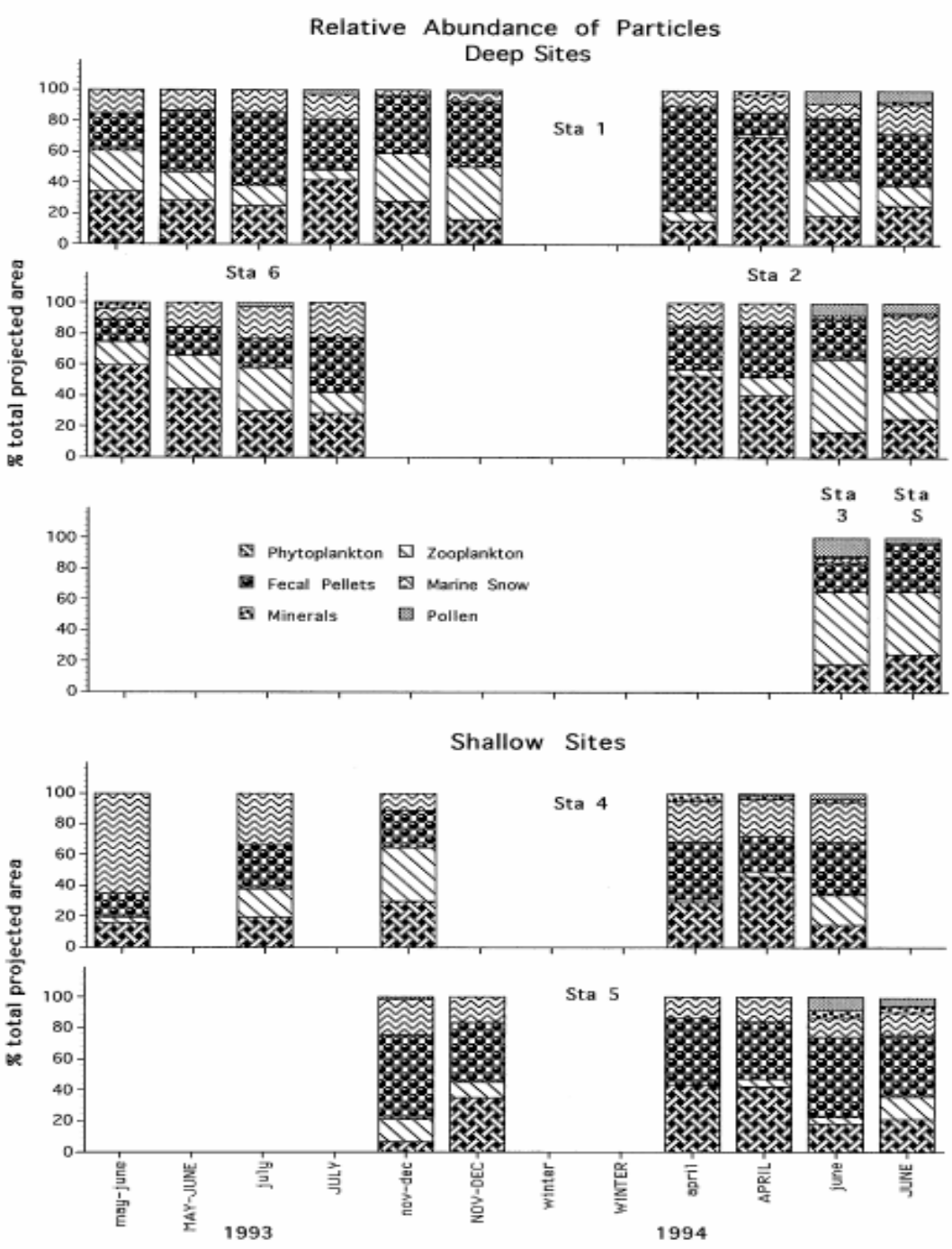

Figure 14. The relative abundance, expressed as the percentage of total particle surface area, of the different classes of particles observed under the microscope. Upper-case letters for the dates are used to refer to samples taken with the large trap, while small-case letters are used for the samples obtained with the small trap. Exceptions are the second sample at St. 2 in “APRIL”, which is in fact another small trap taken one day later, and the St. 3 “June” sample, which came from the large trap.

600 mg C/m^2/d. A weak fall bloom (November-December 1993), however, was, noted at Station 5. If the trap data from these times are grouped together (fig. 11), a clear pattern emerges. Blooms are reflected in the sediment traps by very high (often > 90%) proportions of phytoplankton cells, dominated (except for the late-fall bloom at St. 5) in roughly equal parts by centric and pennate diatoms. A variety of species (of the genus *Thalassiosira*, *Melosira* and *Skeletonema*) comprise the centric diatoms, while two species (*Fragilariopsis* sp. and *F. oceanica*) account for almost all the pennate diatoms. The importance of fecal pellets and, in particular, zooplankton particles is minor.

Post bloom: In June 1994 (fig. 12), phytoplankton numbers were still elevated, but the influence of pennate diatoms was much reduced. A single species, *Thalassiosira nordeskioldii*, dominated the abundant centric diatoms, and dinoflagellate cells were more evident. Zooplankton displayed the greatest diversity during this period: besides the abundant protozoans (tintinnids and formanifera) they included more microzooplankton (crustacean and bivalve larvae, early stages of genus *Calanus* and small cladoceran crustaceans).

Non-bloom: The remaining samples from 1993 are shown in figure 10. For the first time phytoplankton particles tended to form less than half of the total number, with dinoflagellates (*Dynophysis* and *Protoperidinium*) forming a large part. Loose and compact rod-shaped fecal pellets were abundant, oval pellets also were quite evident, and small loose rods characterized the November-December samples. Zooplanktons were more common, consisting mainly of a variety of tintinnids of genus (*Parafavella*, *Ptychocylis*, *Codonella* and *Poroecus*) and *Globigerina* protozoans, and lesser amounts of earlier stages of *Calanus* spp. and small siphonophors.

2. 4 Discussion

2. 4. 1 Reliability of the trap measurements

Absolute flux rates. There is considerable discussion in the literature about what exactly is sampled by sediment traps and how traps may be subject to sampling bias of

different kinds, Gardner (1996). Moored traps may be particularly affected by turbulence at the mouth and even within the trap cylinders themselves (Gust *et al*., 1992, 1994).
We have some confidence that the big (0.5 m^2) drifting trap used in this study on average provides a reasonable estimate of the total mass flux. The instrument has been in use in the Lower St. Lawrence Estuary and Gulf since 1980. There is little doubt that considerable small-scale spatial and temporal variability in the vertical flux exists in this environment. This was confirmed during 2 to 3-week daily deployments of duplicate traps at a repeated site in the Lower Estuary (Lavigne *et al*., 1997). However, when sufficient data have been assembled to provide a relatively long-term average, the large trap results agree with sediment accumulation rates measured independently using radioisotopes in sediment cores (Silverberg *et al*., 1986). The Technicap time-series trap, collecting for 12 months, also agreed with ^{210}Pb sedimentation rates from estuary sediments. A similar result was obtained for the Anticosti Gyre site (Silverberg *et al*., 2000) for which we have the most extensive sediment trap coverage. Such agreement, within a factor of two, with ^{210}Pb-determined sediment accumulation rates, again leads us to believe that, at least in the deep Laurentian Trough environment, at a depth well below that of wind mixing and thermohaline-driven shear, with minimal ambient suspended particulate matter, both the big trap and the Technicap provide reasonable numbers.

Our results show that small (0.03 m^2) cylinders, on the other hand, appear to collect more material per unit area of collecting surface than the large cylinders. Drag effects due to differences in the resistance of the surface float and the relatively smaller drogue action of the small trap (with a damper plate but no sail) are considered to be unimportant (Boyd *et al*., 1997). Elimination of settling particles by detritus feeders (including coprophagy and coprohexy - see Roy *et al*., 2000) in the interval between 50 and 150 m is another mechanism that would reduce the apparent flux in the large traps. However, the relative over sampling was true not only for the small drifting sediment trap at 50 m when compared to the large traps at 150 m depth, but also for the large traps at the same 50 m depth as the small traps, and for the small cylinders mounted directly on the frame of the large drifting trap (fig. 3). Such a tendency for smaller collecting cylinders to sample more flux than large-diameter traps might be related to decreased

Reynolds numbers for the same current speed in moored traps (US GOFS, 1989), but our results suggest that this is a problem that should be pursued with free-drifting traps as well.

Given the "snapshot" nature of the 24-h sediment trap observations, the relatively large standard errors in estimating the total mass flux, as well as the uncertainties in interpreting the flux rates using the small drifting trap, it would be wise to consider our mass and carbon flux results as the first indicators of the vertical transport rates in the Gulf of St. Lawrence. Interpolation to annual fluxes is probably justifiable only for St. 1, where abundant measurements (including 6 months of moored trap data) are available (Silverberg *et al*., 2000).

2. 4. 2 Composition of the settling material

Our drifting traps contained no preservatives, were deployed for 24 h or less, and were not subject to repeated passage of vertical migrators. We present our results herein as "material encountered in the traps". There are a number of indications that the traps reliably represent what was actually sedimenting at the times of collection. To deal with zooplankton "swimmers", we opted in this study for a simple screening-off of organisms > 1 mm. Significant numbers of "swimmers" (dominantly copepods) larger than 1 mm were only encountered in 12 of the 32 drifting trap deployments, and there was no correlation between the number of these swimmers and the number of particles of zooplankton origin (e.g. fecal pellets, mesozooplancton body parts, and microzooplankton). The short deployments of unpoisoned traps may reduce the problem for the Gulf of St. Lawrence, at least for the meso-sized swimmers.

Besides succumbing to preservative solutions and adding their corpses to the bulk of the accumulating sample (Lee *et al*., 1988), swimmers also may contaminate traps by liberating eggs (Michaels *et al*., 1990; Silver and Gowing, 1991). The majority of the eggs encountered in this study, however, were of fishes rather than copepods, and copepods with their egg sacks attached as well as released egg sacks were among the particles removed by the 1 mm screen. Eggs smaller than 1 mm were not sufficiently

numerous to strongly influence the relative numeric or surface area abundances presented in this study.

Organisms other than zooplankton possibly enter sediment traps during vertical migration. Heiskanen (1995), in coastal waters of the Baltic, encountered contamination due to the vertical migration of three dinoflagellate and ciliate species of micro-and nanoplankton size, which she termed “phototrophic swimmers”. Of these, only the ciliate *Eutreptia* sp. occurred in the St. Lawrence, in one trap during the winter of 1993 and in very low abundance.

The small and the large traps apparently sample the same kinds of settling particles. An examination of figs. 10-14 shows that the relative proportion of the different particle types is essentially unchanged between 50 and 150 m depth, or between the large and small traps. This implies that there is not much selective reprocessing of particles between the two depths. The same thing is indicated in the relative abundance and size distribution of the four classes of fecal pellet (fig. 13). The diameters of the majority of fecal pellets encountered appear to be those of copepods, by far the most abundant zooplankton in the upper water column.

Another indication that the trap contents reflect what was happening in the photic zone is the similarity of the relative numeric abundances of the major taxonomic classes of phytoplankton in Niskin bottle samples from the photic zone (Lovejoy *et al*., 2000) and in the two kinds of sediment trap (fig. 15). There are some differences, e.g., in the large traps the relative proportion of centric diatom cells increases slightly, and during April 1994 the pennate diatoms are much less abundant in the large traps than in the small traps, even at St. 5 where both trap models were at the same depth. Also, the “naked ciliates” class is often underrepresented in the traps. These differences are likely related to the different procedures used in the sampling and microscopic identification and the sinking properties of the various algal groups.

We conclude that our trap information about the composition of the material making up the vertical flux is more certain than our estimates of the absolute fluxes, and

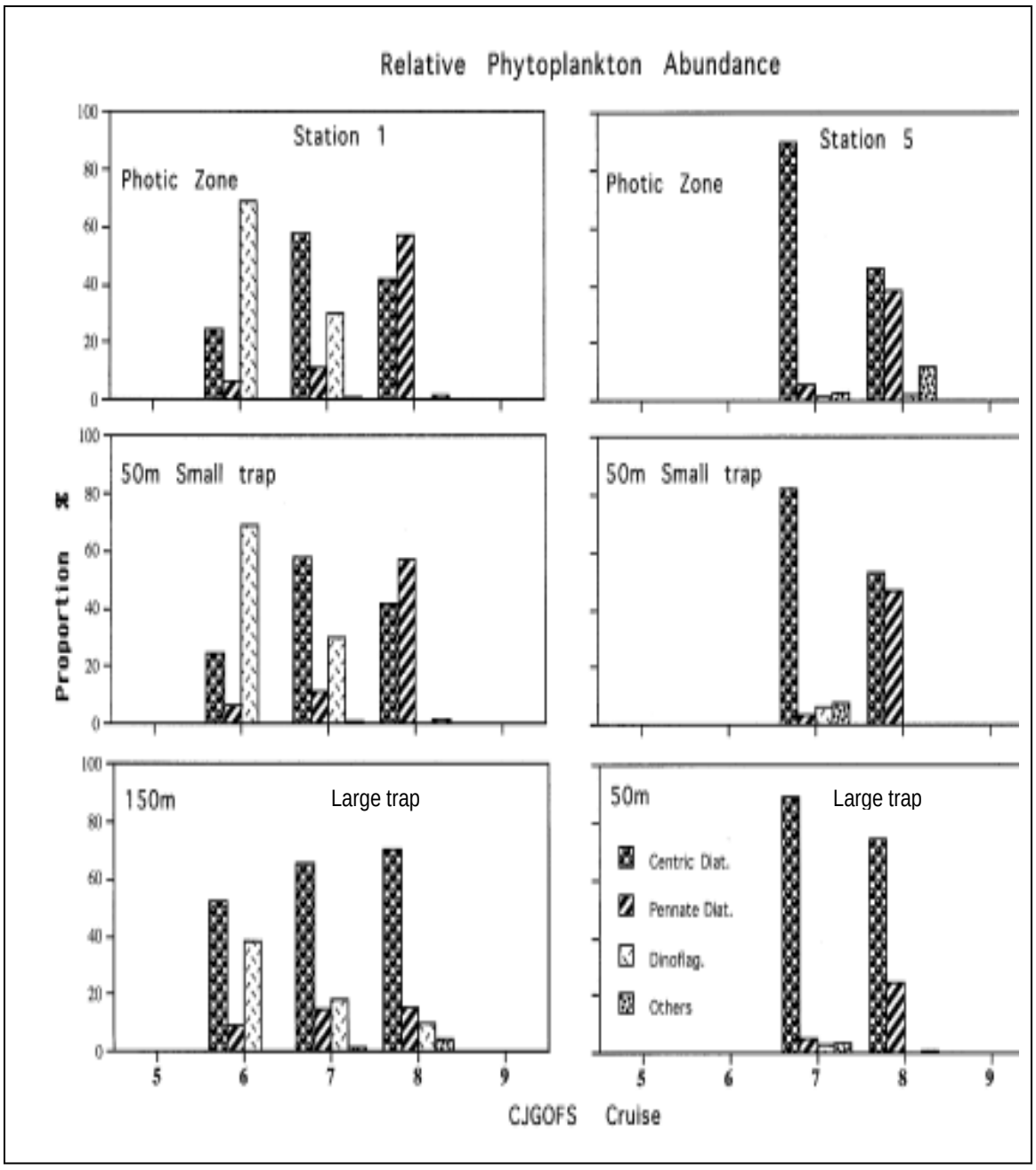

Figure 15. Comparison of the relative numeric abundances of different classes of phytoplankton measured in samples from: photic zone Niskin bottles; the small trap at 50 m depth; and the large trap at 50 or 150 m depth - (a) St. 1 Anticosti Gyre; (b) St. 5 Miscou Channel. The strong resemblance in the overall composition of the phytoplankton indicates that there is no significant bias in the settling of different classes of phytoplankton or selectivity by the sediment traps.

presently also more useful in interpreting shifts in the ecological regime.

2. 4. 3 Factors influencing variations in the composition of the settling particulate matter

The various 24-h traps analyzed for this study indicate that the relative proportion of particle types forming the vertical flux is equally variable at all sites (fig. 14). This apparent lack of geographic distinction, which suggests that the Gulf of St. Lawrence behaves as a single entity, also was observed in other water column studies (Savenkoff *et al.*, 2000), despite variations expectable from the differences in depth and distance from the mouth of the estuary (Doyon and Ingram, 2000). More complete time-series data than the once-a-season sampling of the CJGOFS field program is required to distinguish subtle geographic differences.

Seasonal differences in trophic structure in the water column however, are, well reflected in the composition of the settling particles. Companion studies (Doyon *et al*., 2000; Roy *et al.*, 2000; Savenkoff *et al*., 2000; Tian *et al.*, 2000; Vezina *et al*., 2000) and previously published work (Steven, 1974; Sevigny *et al*., 1979; de-Lafontaine *et al*., 1991; Rivkin *et al.*, 1996; Savenkoff *et al*., 1996) document the occurrence of two distinct seasonal trophic regimes in the water column during the ice-free months, strongly influenced by the development of stratification and the depth of the surface mixed-layer mixed-layer. Phytoplankton blooms occur in the early spring, generally April, when there is ice-melting and dispersion, an increase in light penetration and abundant nutrients, although the mixed layer is still relatively deep. Non-bloom or post-bloom conditions occur during the summer and early fall, when surface warming, aided by the arrival in the Gulf of the fresher water generated during the spring thaw, and milder winds lead to the establishment of a thin mixed layer and a progressive exhaustion of nutrients. Somewhat smaller blooms may occur in the late fall, when light and temperature are still sufficient for phytoplankton to respond to the renewal of nutrients in the euphotic zone as the mixed layer depth increases.

Winter conditions in the Gulf of St. Lawrence consist of cold surface waters 90% ice-cover, mixed by strong winds to a depth greater than 50 m, and short days. Little information is available concerning this season, but phytoplankton would be minimally abundant and zooplankton numbers are presumably reduced, with some species concentrated at the depth of the temperature minimum (Rainville and Marcotte, 1985). The winter time-series trap in the Anticosti Gyre shows levels of total mass flux and total carbon flux similar to that observed during the ice-free seasons. Similar relationships have been observed in the Lower St. Lawrence Estuary (Louchouarn *et al*., 1996). The C/N ratios during the winter, in fact, are somewhat lower than the material collected during the rest of the year. Evidently, mechanisms for the formation of fast-settling particles continue under ice-cover, and organic matter of marine origin is still abundant.

Figure 9 clearly shows the contrast between the high, phytoplankton-driven numerical fluxes during the April bloom, and the lower numeric fluxes, with a mix of fecal pellet and other particles of zooplanktonic origin, during the non-bloom periods of 1993. The June 1994 trap material appears to be more a transition between the two trophic regimes described for the photic zone, and variably displays attributes of both. The late fall bloom is clearly evident only for St. 5. During April 1994 (fig. 10), the dominance of the numeric flux (70-95%) by large phytoplankton (mostly the pennate form, *Fragilariopsis* spp., as well as the genus of centric diatoms *Thalassiosira*, *Chaetoceros* and *Skeletonema*) reflects their abundance in the photic zone (Lovejoy *et al*., 2000). In June 1994 phytoplankton make up only 40-80% of the numbers of sedimenting particles and during the non-bloom samplings of 1993, their relative numeric abundance is reduced to 25-75%. The pennate forms, very abundant in April (some perhaps originating as ice-algae or ice-rafted phytobenthos), are markedly reduced at other times. *Chaetoceros* species, common during April and June and at St. 5 during the late fall, are also sharply reduced during non-bloom periods. During the latter (e.g. May-June, July and November-December, 1993), large dinoflagellates, characteristic of the summer-fall trophic regime (Rivkin *et al*., 1996; Lovejoy *et al*., 2000; Savenkoff *et al*., 2000) are readily apparent in the trap material.

The range of the numeric fluxes of phytoplankton in the present study corresponds to the values reported for environments of relatively low productivity (open ocean, NE Pacific, NE Atlantic - see table 5 and the references therein). However, the highest numeric fluxes measured in the Gulf (April 1994), are comparable to areas of moderate productivity (e.g., Eastern Tropical Pacific, Norwegian fjord). In highly productive areas (such as the upwelling zone of California), reported phytoplankton cell fluxes are one to two orders of magnitude higher. At roughly 150-200 $gC/m^2/yr$ (Steven, 1974; de-Lafontaine *et al*., 1991; Savenkoff *et al*., 1996; Tian *et al*., 2000;) the annual primary productivity in the Gulf is considered moderate to high. The lack of a correspondingly high numeric flux of phytoplankton cells could be interpreted in various ways. The massive sinking associated with phytoplankton aggregation (Alldredge and Gotschalk, 1989; Passow *et al*., 1994) may not be common in the Gulf of St. Lawrence. Alternatively, massive sinking may occur, but the timing of our one-day per site sampling missed any such events. Phytoplankton may be heavily grazed and broken up into fragments too small for our identification procedure and dispersed within the marine snow or hidden in fecal pellets -phaeopigment proportions in the traps are greatest during bloom periods, indicating increased herbivory at the same time (Roy *et al*., 2000). Lateral, rather than vertical export also may be a factor. Zakardjian *et al*. (1999) have shown that surface currents in the Lower St. Lawrence Estuary are sufficient to produce considerable advection of phytoplankton.

Phytoplankton are quite small, however, and their contribution to the abundance (2D projected area) of the sedimenting material averages only about 30% (fig. 14). A low contribution also was found by Roy *et al*. (2000) using chlorophyll a as an indicator of the presence of phytoplankton in the traps. The true influence of the diatom blooms on the settling particulates awaits electron microscope analysis of the marine snow and the contents of the fecal pellets, since it is likely that the resistant siliceous cell walls, even as debris, would more closely preserve a phytoplanktonic origin than its highly labile organic matter.

Fecal pellets are a major component of the vertical flux, accounting for approximately

one-third of the 2D area of the particles in the traps, regardless of season or depth. Interestingly, in contrast to the phytoplankton numbers, the numeric fluxes of fecal pellets in the Gulf are high, similar or greater than reported from other coastal or continental margin areas (table 5). This is likely related to the high zooplankton biomass (on average 2-5 gC/m^2 throughout the ice-free season -Savenkoff *et al*., 2000) compared to other coastal environments (de-Lafontaine *et al*., 1991). The high proportion of fecal pellets in all seasons is in agreement with the ability of calanoid and larvacean zooplankton to change their diet as the trophic structure shifts (Urban *et al*., 1992). Similarly, Vézina *et al.* (2000) model strong trophic links between microzooplankton, which are the dominant herbivores throughout the year, and mesozooplankton. We do not have a clear interpretation of the origin of the various forms of the pellets encountered. Loose and compact rods generally occur in roughly equal proportions and may be alternately produced according to how quickly individual zooplankton process a particular feeding event. Both have been observed in ship-board incubations of calanoid copepods. Mid-sized calanoid copepods dominate the zooplankton biomass in this region (Roy *et al*., 2000). Similarly, the origin of oval pellets is difficult to assign. This form has been attributed to *Oithona similis* (Martens, 1978; González *et al*., 1994), a small species abundant at all of the sites in the Gulf (Roy *et al*., 2000), but Smetacek (1980) observed that this copepod produces small "detrital clumps". Bathmann *et al*. (1990) assigned them to ostracods, while Deibel, 1995 (personal communication) identified some of the oval pellets in our samples as *Oikopleura* feces. The occurrence of oval pellets in all fecal diameter classes suggests a multi-species origin for these pellets.

Fecal pellet diameters of 50-109 µm, the most abundant at all times and sites (fig. 13), are of the size generated by calanoid copepods. Larger diameters (110-200 µm), such as would be generated by euphausids and other macrozooplankton (>2000 µm in size), are only found sporadically. They tend to be more abundant during the non-bloom periods (average 7.2%), but the variability is high. At St. 1, no large pellets were collected during April 1994, but they accounted for an average of 5.6% for the other sampling periods. The unique appearance of abundant small loose rods during the November-December 1993 cruise, occurred when the small copepod *Oithona similis* was

particularly abundant in the water column, together with *Microcalanus pusillus*, another small copepod (Roy *et al*., 2000). The fecal pellet diameters do not reveal the shift to more abundant, smaller mesozooplancton during the non-bloom periods (Savenkoff *et al*., 2000), nor the prevalence of smaller zooplankton species at the shallow sites (fig. 13). Station 4, however, showed an absence of compact rods during May-June 1993, and a generally greater proportion of marine snow (fig. 13), which may reflect the production of more fragile pellets. The generally higher mesozooplankton standing stock at the shallow sites is partially reflected by the relatively high numeric fluxes of fecal pellets at Sts. 4 and 5 during November-December 1993 and June 1994 (fig. 9). Recycling of fecal material during its descent through the water column may complicate the attribution of individual forms to specific zooplankton stocks.

Roy *et al*. (2000) have noted strong differences between the incubation-determined rate of fecal pellet carbon excretion by copepods in the upper layers of the water column, and the corresponding fluxes in the small sediment traps at 50 m and the large traps at 150 m. In general, the fecal C flux in small traps at 50 m accounted for a 60-150% of their calculated rate of production in the overlying water column, while the large traps at 150 m only accounted for about 5%. This implies that most of the fecal pellet production suffered severe degradation (via bacterial degradation; e.g. Martens and Krause, 1990) or physical breakdown (e.g. coprophagy, coprohexy) during their passage through intermediate depths (Noji, 1991). However, the fecal C fluxes calculated for the concurrent large traps at the same 50 m depth as the small traps at Sts. 4 and 5, showed an average fecal C flux to production proportions of 5.2%, the same as for the large traps at 150 m. Although the small traps may be compared with each other, their tendency to over sample both total dry weight and fecal pellets means that the actual proportion of vertically sedimenting fecal pellets is closer to that recorded by the big traps. Thus, the conclusion that the fate of most of the mesozooplancton fecal pellets produced in the water column is to be degraded, is even more strongly supported by the data from the big traps.

Marine snow, the term we have used in this study to refer only to the fine-grained

matrix of fluffy aggregates remaining after sample manipulation, averaged about 15% of the 2D abundance of the particulate matter under the microscope, but varied over a broad range (2-65%). These numbers are the most heavily biased in relation to their actual contribution to the total mass flux, since the density of fresh marine snow has been estimated at about 100 μg/cm^3 (Alldredge and Gotschalk, 1989; Alldredge, 1998), about ten thousand times less dense than fecal pellets (about 1.1 g/cm^3, Silver and Gowing, 1991). The relative proportions therefore should be used only as an indicator of the relative availability of polysaccharide "glue" and included fine-grained detritus. Future studies in the Gulf should profit from new colorimetric techniques to estimate transparent exopolymer particles, or TEP (Passow *et al.*, 1994). There is a weak negative correlation ($r = 0.46$, $P = 0.05$) between marine snow abundance and that of zooplankton, suggesting that snow is subject to zooplankton grazing. On the other hand, the highest snow contents were observed at the Magdalene Shelf site (St. 4), where Roy *et al.* (2000) have noted higher proportions of smaller-sized copepods, which may generate more snow through the break up of more fragile fecal pellets.

Models of the vertical export of biogenic carbon from the photic zone have tended to assume that direct sinking of zooplankton, or their detritus apart from fecal pellets, is not a significant component of the vertical flux zone (Rivkin *et al.*, 1996; Vézina *et al.*, 2000). The abundance of apparently intact microzooplankton (mainly tintinnids, larval forms and eggs) as well as foraminifera and various mesozooplankton body parts in our samples (on average 15% of 2D projected area) suggests that such direct zooplankton sinking merits further investigation. While some of these forms (e.g. copepod eggs) might be excluded from the vertical flux on the grounds that they may be released by copepod swimmers that die after entering sediment traps (Silver and Gowing, 1991) or that may enter traps during vertical migration (Michaels *et al.*, 1990), the living components of zooplankton cannot all be excluded when analyzing trap material (Silver and Gowing, 1991). Nor is it certain that they should be. A succession of organisms have been found to colonize large aggregates (Silver *et al.*, 1984), and other small organisms are likely attracted by the relatively labile organic matter, or become attached, voluntarily or not (Shanks and Edmonson, 1990). The traps used in this study were deployed for only

24 h, not much time to be encountered by diel migrating organisms, and contained no preservative solution to encourage either the rapid death of swimmers or their release of eggs. In fact, a majority of the eggs encountered in the Gulf traps were of fishes rather than copepods. The problem of the microzooplankton component of trap material will require considerably more attention before it is eventually resolved, for it is probable that many living organisms actively or passively become associated with the food-rich complex aggregates of marine snow, phytoplankton and fecal matter, and that their fate is to sink along with the rest of the particulate debris in the coastal ocean.

A similar association of abundant microzooplankton in non-poisoned traps dominated by fecal pellets has been reported from the Bjornafjorden (González *et al.*, 1994). We must assume that a large portion of the many microzooplankton particles we have observed in the traps form part of the true vertical flux. During non-bloom periods, these make up a significant portion of either the numbers or abundance of settling material, particularly when ignoring pollen grains and marine snow (figs. 10-12). During the April 1994 spring bloom, they accounted for an average of only 4% of the total particulate 2D surface area, but averaged 20% for the other sampling periods. Together with dinoflagellates (grouped with the phytoplankton in our counts, although mostly non-autotrophs) their abundance in the traps confirm the dominantly heterotrophic trophic regime in the water column during non-bloom periods.

Regardless of the limitations of the small number of measurements of absolute fluxes, the CJGOFS sediment trap record provides a good picture of the composition of the settling particles. This clearly points to a very strong influence on the vertical flux of particulate matter by material of zooplanktonic origin, both in the form of mesozooplankton feces and microzooplankton body parts. Direct settling of phytoplankton cells is numerically important only during the bloom and post-bloom periods. Much of the primary organic matter produced during photosynthesis must therefore be transformed by heterotrophs before escaping from the surface and intermediate waters.

CHAPTRE III

VECTORS OF CARBON TRANSPORT

CHAPTER III -VECTORS OF CARBON TRANSPORT

3. The contribution of various types of settling particles to the flux of organic carbon in the Gulf of St. Lawrence

3.1 Abstract

The contents of 32 free-drifting sediment traps deployed in the Gulf of St. Lawrence (GSL) have been analyzed for particulate organic carbon (POC) and the C contribution of the different types of particles found in the traps. Two trap models were used in 1993-1994: small traps at 50 m and larger traps at 50 and 150 m. Absolute mean fluxes of POC (42 and 149 mg C m^{-2} d^{-1} on the larger and small, traps respectively), of C attributed to fecal pellets (6 and 60 mg C m^{-2} d^{-1}) and of C attributed to phytoplankton (3.2 – 42.9 mg C m^{-2} d^{-1}) were all in the same range as those encountered in regions of moderate productivity. Fecal pellets were the major component of this flux, with an important contribution of microzooplankton, particularly during the summer of 1994. The **c**ontribution of phytoplankton to the flux of POC was lightly less that one of fecal pellets**.** The identification of algal groups that are part of this flux led to recognition of three trophic regimes already identified from water column studies: (1) a period when diatoms were dominant during the spring, (2) a longer interval, which was dominated by dinoflagellates at most others times of the year, and (3) a period of transition during summer. Although the contribution of marine snow was estimated, its real importance in the vertical flux of POC remains uncertain. The vertical flux of C attributable at the GSL is dominated by components of animal origin.

3. 2 Introduction

Knowledge about the export of particulate matter and its biogenic components from the surface layer of the ocean is important for understanding the role of the ocean in the global C cycle (Fenchel 1988; Hedges *et al*., 1998; Valiela, 1995; Turner, 2000) and global warming. One of the parameters needed in models of the ocean C cycle is the rate of sequestration of excess atmospheric CO_2 via sedimentation and isolation of organic C in the deeper parts of the ocean. (e.g. Berner, 1982; Silverberg *et al.*, 2000).

Another key aspect in understanding the ocean C cycle is the maintenance of an equilibrium, in the long term, between the losses of organic nitrogen from the euphotic layer, and the replacement of inorganic nutrients from upwelling and mixing from deeper waters, which support an equivalent rate of "new" primary production (Eppley and Peterson, 1979).

Changes in the trophic regime are complex in all marine regions (Lalli and Parsons, 1993; Rivkin *et al.*, 1996) and knowledge about the nature of sedimenting particles may help in understanding which mechanisms are important in the different regions and times of the year. Particles implicated in the vertical transport include large phytoplankton cells and diatom aggregates, fecal pellets, micro-organisms and aggregates of marine snow (Honjo, 1980; Angel, 1984; Fowler and Knauer, 1986; Alldredge and Silver, 1989; Silver and Gowing, 1991; Romero *et al*,. 2000).

Numerous other studies on settling particulate matter have reported on the mass and carbon fluxes in the ocean. In general, more information has been published concerning in the phenomenon in open ocean (e.g. Knauer *et al.*, 1979; Honjo, 1980; Deuser *et al.*, 1981; Knauer and Martin, 1981; Honjo, 1982; Hargrave, 1985; Deuser, 1986; Fowler and Knauer, 1986; Martin *et al*., 1987; Karl *et al*., 1988; Lohrenz *et al*., 1992; Murray *et al.*, 1997). Less has been published concerning coastal waters (Dunbar and Berger, 1981; Hedges *et al*., 1988; González, 1994b; Buck and Newton, 1995;

Lundsgaard and Olesen,. 1997). Although some of these studies report on the contribution to the POC flux of specific of particles (Turner 1997; Honjo and Roman, 1978; Bruland and Silver, 1981; Fowler and Knauer, 1986; Turner, 2000) such information is rare and fragmented, for both the open ocean and the coastal zone. The most comprehensive study, assigning contributions to all of the components of trap material, is that of Silver and Gowing (1991).

Less productive (oligotrophic) marine environments, such as the open ocean where long food chains and small size organisms dominate (Azam, 1983; Fenchel, 1988), tend to transfer to depth less organic material than more productive (eutrophic) environments, such as coastal and upwelling regions with shorter food chains and larger size microorganisms (Eppley and Peterson 1979; Silver and Gowing 1991; Lalli and Parsons 1993). Some studies suggest that the vertical flux is dominated by particles of zooplanktonic origin (e.g. Urrère and Knauer, 1981; Noji, 1991), while others suggest that some form of aggregation of phytoplankton cells accounts for the massive sinking of organic carbon (Rice *et al.,* 1986; Alldredge and Gotschalk, 1989; Passow *et al.,* 1994).

The Gulf of St. Lawrence, where the present study was undertaken, is unique in possessing both oceanic and coastal characteristics (Therriault, 1991), making it an excellent region to study the marine carbon cycle. There are several earlier studies published on the carbon cycle and particle fluxes in the Gulf and Estuary of St. Lawrence, mainly for the deep Laurentian Channel. These include total mass and carbon fluxes (Hargrave and Prouse, 1981; Syvitski *et al.,* 1983; Silverberg *et al.,* 1986; Hargrave, 1994) and the organic geochemistry of settling particles and sediments (Silverberg *et al.,* 1985; Colombo *et al*., 1996; 1997ab, Lavigne *et al.,* 1997; Colombo *et al*., 1998).

For the spring and early summer period, Rivkin *et al*. (1996) described two distinct trophic regimes: a) a spring phytoplankton bloom when herbivory dominates, and b) a post-bloom period when the microbial food web and omnivory dominate. Interestingly the vertical carbon fluxes were similar during both periods. This alternation

between bloom and non bloom periods was also observed by others working in this region (Savenkoff *et al.*, 1996, 2000; Vezina *et al*., 2000). Roy *et al*. (2000) reported the first directed measures and calculation of the estimates of carbon content of fecal pellets from the Gulf of St. Lawrence (GSL) at 50 and 150 m, signaling the importance of this type of particle as a vector for transfer of carbon in this region.

The nature of the large particles collected in the sediment traps deployed in the GSL during this study was described in a previous chapter of this thesis (Romero *et al*., 2000). The types of large particles encountered, as well as their numeric fluxes, distinguished three periods over the duration of the study: (1) algal blooms, with major numeric fluxes of phytoplankton, dominated by centric and pennates diatoms, (2) post-bloom periods, with fewer phytoplankton which are dominated by centric diatoms, and (3) non-bloom periods, with a heterogeneous mix of particles (dinoflagellates, fecal pellets, microzooplankton). Fecal pellets were identified as the most evident vector in the GSL.

The carbon contribution of each of these flux components has never been presented for the GSL. This missing information is essential for the understanding of the biological processes and trophic regimes that control the flux of particulate organic material in the GSL. The objective of the present work was thus to estimate the carbon contribution of the particles that participate in the vertical flux of organic matter in the GSL.

3. 3 Materials and Methods

This study was located in the GSL, shown in Figure 1 of Romero *et al.* (2000, and Chap. 2 of the present thesis). For the present work, only the stations located inside the GSL were considered. Two types of free-drifting sediment traps (fig. 2) were used to sample the sedimenting particles: a) small traps, consisting of four identical cylindrical plexiglas tubes measuring 98 cm in length and 10.2 cm in internal diameter, fitted on a metallic cross with a 35 kg ballast weight underneath, and b) large traps, consisting of four PVC cylinders, each measuring 30 x 150 cm (with a collecting surface of 1/8 m^2)

mounted on an aluminium structure with a weighted (30 kg) oscillating plate at the bottom and a 2 m^2 sail (Silverberg *et al*., 1985). This design allowed for minimum drag and vertical positioning in the water. The small traps were submerged at 50 m, while the large traps were either deployed at 50 m or at 150 m. Other technical details, as well as trap-handling procedures and sample manipulation, can be found in Romero *et al.* (2000).

Once the fraction ('split') of the total sample destined for microscopy was obtained, a sub-sample of 1 ml was withdrawn after mixing, and this sub-sample was collected in the bottom slide of phytoplankton sedimentation chambers (Hasle, 1978). All the particles present in these sub-samples were identified, counted and measured using a Zeiss Axiovert-100 inverted microscope. While length and width were easy to measure, the third dimension (height) could not be measured directly, although it is essential for volume estimates, which can then be transformed into carbon values. Hence, volume estimates were calculated in the manner described below.

The algorithms that were used to estimate the volume and carbon content of particles are given in table 6 for each major type of particles (phytoplankton, fecal pellets, zooplankton and pollen).

Phytoplankton. Volume estimates were based on geometric forms closest to those of the algal cells observed: Cylinder: this form was used for centric diatoms, unicellular or in chains. For unicellular diatoms, a short cylinder form was used with the same formula, except that "h" (height, thickness) was obtained from the literature (electronic microscope measurements: Hasle and Lange (1992). Rectangular box: this shape was used for a few centric diatoms and most pennate diatoms. Ellipsoid: this shape was only used for two genera of pennate diatoms. Cube: this shape was used for the only two species of silicoflagellates encountered and the few large-sized nanoflagellates named 'others' in the text.

For the estimation of phytoplankton carbon, the equation of Strathmann (1967) was used with the modification recommended by Sicko-Goad *et al*. (1984), which reduces the carbon content by a factor of 0.54 to account for the presence of the vacuole. The attribution of carbon for phytoplankton was made a second time, using the more recent relationships determined by Menden-Deuser and Lessard (2000).

Table 6 Formulas for estimated volume of different classes of particles and their respective equations for carbon calculations

Geometric Forms of particles	Area	Volumen	Silver and Gowing (1991)´s Modifications of Strathmann´s Regression pg carbon/ cell	Menden-Deuer and Lessard (2000) Células > 10^3 µm^3 C = Pico-grams of carbon/ cell	Menden-Deuser and Lessard (2000) parameters		microscopic measures		volume unites
					log a	b			
Pennate Diatoms									
Rectangular Prism	(L)*(l)	$(L)*(l)^2$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)	-0,993	0,881	L = length	l = width	V = Volume (μm^3)
Ellipse		$4/3\ Pi(a)^2\ b$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)			a = short axis	b = long axis	V = Volume (μm^3)
Centrics Diatoms									
Cylinder (single)	$Pi*R^2$	$Pi(D/2)^2\ H$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)			D = diameter	h = width **$**	V = Volume (μm^3)
Rectangular prism (chain-form.)	(L)*(l)	$(L)*(l)^2$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)			L = length of chain	l = width of chain	V = Volume (μm^3)
Dinoflagellates									
Rectangular prism	(L)*(l)	$(L)*(l)^2$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)	-0,1190	0,819	L = length	l = width	V = Volume (μm^3)
Silicoflagelates									
Cube	L^2	$(L)^3$	Log C= - 0.460+0.866 (logV)	Log pgC cell = log a+ b (log V)	-0,694	1,218	L = length		
Fish´s eggs									
Sphere	$4/3\ Pi\ R^2$	$4/3\ Pi\ R^3$	pgC = V * 0.1 **$ $**				R = 1/2 diameter		
Microzooplankton (Non Tintinnid)							L = length	l = width	V = Volume (μm^3)
Larval forms of mollusks, Crustaceans	(L)*(l)	$(L)*(l)^2$	pgC =V * 5.25*10^-2				L = length	l = width	V = Volume (μm^3)
Tintinnid protozoans	(L)*(l)	$(L)*(l)^2$	pgC =V * 5.25*10^-2				L = length	l = width	V = Volume (μm^3)
Mesozooplankton									
Siphonophores, copepods.	(L)*(l)	$(L)*(l)^2$	pgC =V * 5.25*10^-2				L = length	l = width	V = Volume (μm^3)
Pollen $ $ $	(L)*(l)	$(L)*(l)^2$	Log C= - 0.460+0.866 (logV)				L = length	l = width	V = Volume (μm^3)

$ Hasle and Lange (1992)

$ $ From copepods eggs (Runge, 1984) *in* Silver and Gowing (1991)

$ $ $ Assumed equivalent to diatoms

The results (table 7) were comparable, except that the carbon contributions of dinoflagellates and silicoflagellates were slightly greater using the newer algorithms, and these were used for subsequent treatments.

Fecal Pellets. Volume estimates were based on two geometric forms: Cylinder: this shape was used for compact and non compact fecal pellets. Ellipsoid: this shape was used only for oval fecal pellets. For the estimation of the carbon content, the algorithms of Silver and Gowing (1991) were followed.

Zooplankton. Volume estimates were based on two geometric forms: Rectangular box: this shape was used for all microzooplankton organisms and the small mesozooplankton. Sphere: only the volume of fish eggs were estimated using this shape For the estimation of the carbon content of zooplankton, the approach used by Silver and Gowing (1991) was followed.

Pollen. Volume estimates for pollen grains were based on the shape of a rectangular box, and the Strathmann (1967) equation.

Other considerations: Copepods larger than 1 mm were eliminated from the calculations, since it was assumed that these few organisms had not been efficiently screened out with the 1 mm mesh used to remove the 'swimmers'. Even so, because some of the results gave extremely high volumes for whole mesozooplankton, the entire contents of three of the original splits (50-70 ml) were specifically examined to determine the total number of whole mesozooplankton <1mm. The counts showed that counts of the 1 ml sub samples overestimated this class of particle by a factor of 2-3. Division by 2.5 was therefore applied to the data for this component for all of the samples

The carbon value of shed fragments from crustaceans, which were essentially empty but which accounted for some of the detrital organic carbon, was divided by 10 for the thin and long fragments (such as legs of crustaceans) and by 2 for the wider fragments (e.g. copepod exuviae). In the small traps, which often provided very small samples, errors of manipulation and pipetting appeared to lead to exaggerated values of carbon. For tintinnids, only one third of the observed loricas were actually filled, and hence carbon estimates were reduced to one-third of the calculated value.

Table 7. Contributions in carbon calculate with the Menden-Deuer and Lessard (2000) equation and the Strathmann (1967) equation modified by Silver and Gowing (1991)

Cruise - Station - Trap Type of Particule	mgC/ Split Strathmann (1967) modif. by Silver and Gowing (1991)	mgC/ Split Menden-Deuer and Lessard (2000)
June/94 - St."s"- Large		
Diatoms centric (circle)	0,0160	0,0106
Diatoms centric (rec. boxt)	0,0044	0,0033
Diatoms pennates (rec. box.)	nd	nd
Diatoms pennates (ellipsoid)	nd	nd
Dinoflagellates (rec. box.)	0,2258	0,2590
Silicoflagellate (cube)	0,0019	0,0046
Others	0,0120	0,0118
Nov/93 - St. 5 - Large		
Diatoms centric (circle)	0,0264	0,0174
Diatoms centric (rec. box.)	0,0210	0,0136
Diatoms pennates (rec. box.)	0,0013	0,0007
Diatoms pennates (ellipsoid)	0,0001	0,0001
Dinoflagellates (rec. box.)	0,1497	0,1584
Silicoflagellate (cube)	0,0014	0,0028
Others		
June/94 - St. 1 - Large		
Diatoms centric (circle)	0,0135	0,0089
Diatoms centric (rec. boxt)	0,0261	0,0171
Diatoms pennates (rec. box.)	nd	nd
Diatoms pennates (ellipsoid)	0,0001	0,0000
Dinoflagellates (rec. box.)	0,0197	0,0243
Silicoflagellate (cube)	nd	nd
Others	0,0043	0,0041
April/94 - St. 5 - Small		
Diatoms centric (circle)	0,0022	0,0014
Diatoms centric (rec. boxt)	0,0097	0,0064
Diatoms pennates (rec. box.)	nd	nd
Diatoms pennates (ellipsoid)	0,0022	0,0014
Dinoflagellates (rec. box.)	0,0021	0,0014
Silicoflagellate (cube)	0,0003	0,0010
Others	nd	nd

Foraminifera (*Globigerina*) were eliminated from the calculations, since no protoplasm was observed in the shells. The contribution of their calcium carbonate shells was determined independently and included in the direct carbonate determinations of trap material (Mucci *et al*., 2000). For bivalve larvae, the carbon content estimate was reduced by 50% because about half is found in the $CaCO_3$ of the valves. The carbon estimates for fish eggs encountered in stations 2b in April 1994 and 1s in June 1994 were taken from the average values found for fish eggs in rest of the stations of each cruise, because the very high counts of fish eggs in those two stations were suspect, possibly due to errors during the sample splitting procedures or with pipetting.

Component carbon contents and fluxes were then determined by summing all of the carbon contributions for each class of particle counted and corrected for sub sample and split size. Following Silver and Gowing (1991), marine snow carbon was calculated by subtracting the total "attributed" carbon from the independently determined (CHN analysis of another split) total carbon in the sediment trap.

3. 4 Results

3.4.1. Absolute fluxes attributed to the measured components of the sedimenting material

The absolute carbon fluxes assigned to the different types of particles, expressed in mg C m^{-2} d^{-1}, are shown in figure16, for the various stations and times of the year sampled. The major contributors are clearly fecal pellets and phytoplankton. Total C fluxes measured by CHN analyses (Romero *et al.*, 2000) are generally much higher because they include a contribution from marine snow, which is not included here (see Discussion). There are no discernible geographic trends between stations. Notwithstanding the generally higher fluxes estimated for the small traps (note the 10-fold difference in the vertical scales in fig. 16), and the evaluation of this difference discussed in Romero *et al*. (2000), both trap models showed relatively small combined C fluxes during May-June 1993 (cruise 5) and April 1994 (cruise 8), and larger fluxes during June 1994 (cruise 9), during which microzooplankton, mesozooplancton, detritus and fish eggs were most evident. A few larger fluxes were also observed during spring,

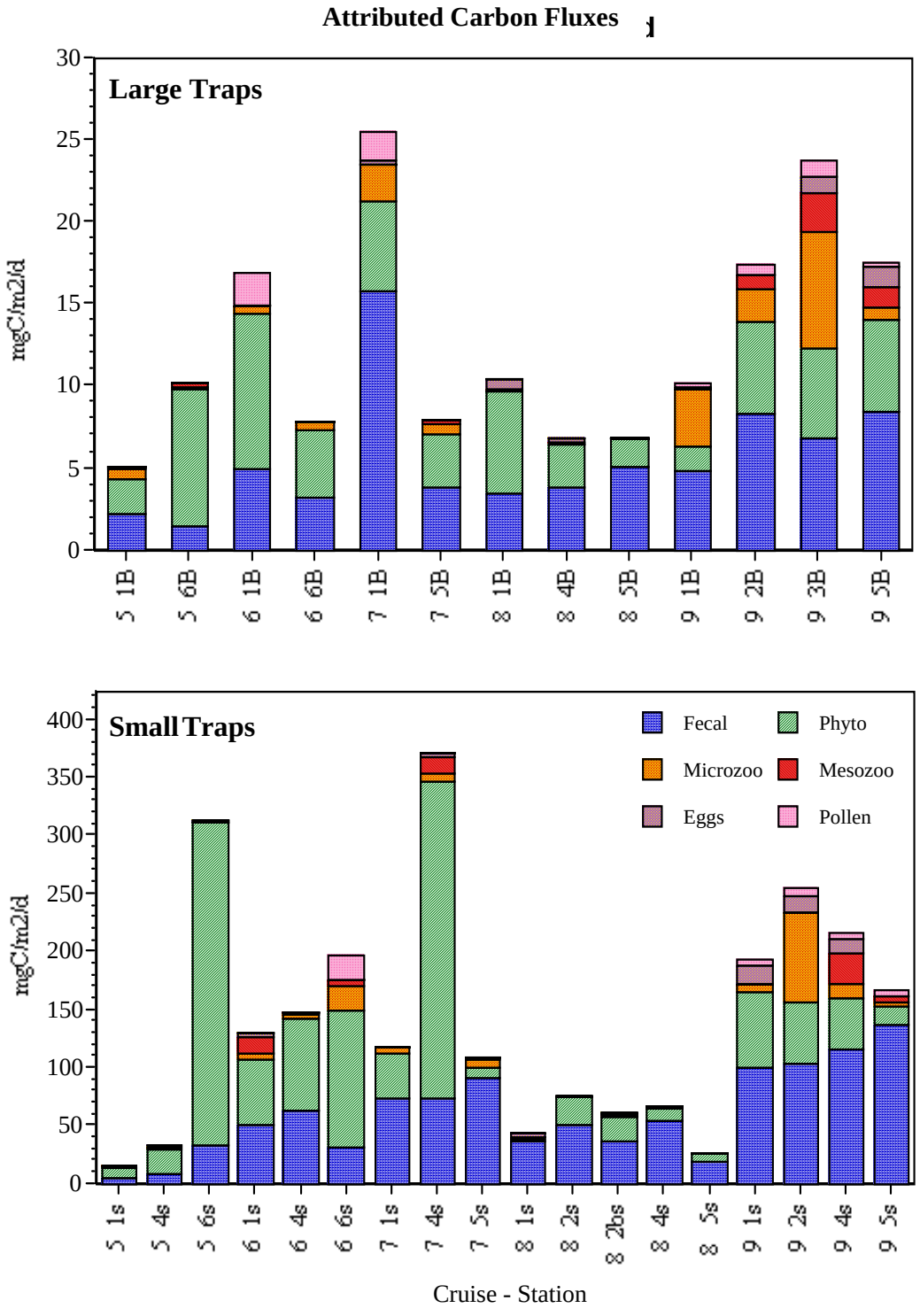

Figure 16 Absolute fluxes carbon attributed to different key particle classes in large and small traps

summer and fall of 1993 (cruises 5, 6 and 7), when phytoplankton were strong contributors.

To situate the Gulf of St. Lawrence among systems of different productivity and to compare the carbon fluxes, table 8 presents the mean and range of POC flux and the percent of primary production it represents, as well as the fluxes associated with fecal pellets and phytoplankton for various sites described in the literature.

The flux levels in the Gulf lie between those of low productivity open ocean areas and moderately productive seas. This is more clearly seen in figure 17, where the GSL total POC fluxes are comparable with those found in some other continental margin areas and oligotrophic open ocean sites.

Marine Snow The estimated fluxes of marine snow carbon (calculated as the difference between CHN-determined total carbon and the sum of all "attributed" component carbon, including inorganic carbon) are shown in table 9. Snow often represents the most important carrier of sinking carbon, surpassing the carbon contribution of fecal pellets and phytoplankton. The negative values (i.e. the sum of the measured components is greater than the CHN-determined carbon fluxes), however, indicate that there are significant uncertainties in the procedures used to estimate the contributions of the microscopically-measured particles. This is considered in more detail in the Discussion section.

3. 4. 2 Relative contributions of the flux components

In order to mitigate the effect of this uncertainty in the absolute fluxes (as well as the tendency of the small traps to over sample total flux and fecal pellets – see Romero *et al*., 2000), the attributed fluxes are compared among themselves (i.e. the sum of their contributions is taken as 100%).The comparison of the main particle classes is shown in figure 18. Fecal pellets are clearly an important vector for carbon transport in the GSL, but the phytoplankton contribution can at times dominate. Zooplankton rarely account for more than 20% of the flux, except in the case of some traps in June 1994 (cruise 9).

Table 8 Absolute Fluxes of Organic Carbon (mg C m^{-2} d^{-1})

Area / Trap Depth	POC Range	POC Mean	% P.P.	Fecal Range	Fecal Mean	% P.P.	Phytoplankton Range	Phytoplankton Mean	% P.P.	Primary Prod'n (P.P.)	Reference	Observations
Gulf of St. Lawrence												
Large traps 50,150 m (n=13)	9 -118	42	10,2	1,5 -16	6	1,4	1,6 -9,4	3,2	0,8	411	*This study, and*	Deep
Small traps 50 m (n=18)	74 - 298	149	36,3	5 -138	60	14,6	3,2 - 279	42,9	10,4	411	Romero *et al* ., 2000	inland sea
Bjornafjorden, Norway												
50 m	20 - 50	31		5 - 52,5	27		0,13 - 0,90	0,57			González *et al* .,	Fjord
100 m	25 -125	50		50 - 225	80		0,46 - 3,16	1,21			1994	
Dabob Bay, Wash. 60 m	18 - 572	385	47,0	77-337	184	22,4	nd			820	Buck and Newton, 1995	Deep inland sea
N. Norwegian Shelf												
60 m spring	30 -117	50	3,3	0.5 - 27	8	0,5	1 - 11	4	0,3	1500	Peinert, 1986	Coastal
summer	17 - 66	30		29 - 77	44	17,6	0,1 - 7	3	1,2	250		
N. Baltic Sea 15-20 m												
Bay	32 - 37	34		0,07 - 0,16	0,11		nd				Viitassalo *et al* .,	Shallow
Archipelago	105 - 224	146		0,02 - 0,10	0,06		nd				1999	inland sea
Open Baltic	112 - 189	150	11,5	0,02 - 0,09	0,05	0,0	nd			1300		
S. Kattegat, Denmark											Lundsgaard and	Shallow
> 22 m (pycnocline)	218 - 349	288		37 - 59	49		nd				Olesen, 1997	inland sea
Sea of Japan												
50-150m	35 - 54	42		0,23 -0,35	0,19		nd				Ayukai and Hatteri, 1992	off Shikoku I.
Voering Plateau												
100-300m may	36185	7		0 - 10	4		nd				Bathmann	Open
june	90 - 275	182		0 - 40	15		nd				*et al* ., 1987	Norwegian Sea
N.E. Pacific												
Santa Barbara Basin 341 m	60			47			nd				Dunbar and Berger, 1981	Calif. Margin
VERTEX (V5C)												
50 - 225 m	335		29,4	4 , 7	5,5	0,5	13,0 - 234	122	10,7	1140		Calif. Margin
VERTEX (V1)												
50 - 300 m	212		40,8	4, 5	4,5	0,9	nd			520	Silver & Gowing, 1991	Calif. Margin
VERTEX (V5B)												
130-300m	70		21,5	4, 5	4,5	1,4	0,6 - 8,4	4,5	1,4	325		Calif. Margin
VERTEX (V2)												
80-200m	38		5,0	0-7,5	3,8	0,5	nd			760		Mexico Margin
VERTEX (V3)												
80-200m	47		10,0	2--5	3,5	0,7	7--23	15	3,2	470		Mexico Margin
VERTEX (V4)												
50 -- 300 m	29		7,3	0-2	1,0	0,3	nd			400		Open ocean
VERTEX (V5A)												
150-275m	41		16,7	0-1	0,5	0,2	0,26 -1,3	0,78	0,3	245		Open ocean
Sub.-tropical Atlantic												
120m	3,4			nd			0,02 - 0,33	0,15			Passow and	Open ocean
324 m	2,4			nd			0,02 - 0,10	0,06			Peinert, 1993	
Weddell Sea											Nothig and	
(50 -300m) Jan-Feb	15 -135	69		nd			0,3 - 5,6	3,4			Bodungen, 1989	Open ocean

Reported POC Fluxes from sub-pycnocline sediment trap

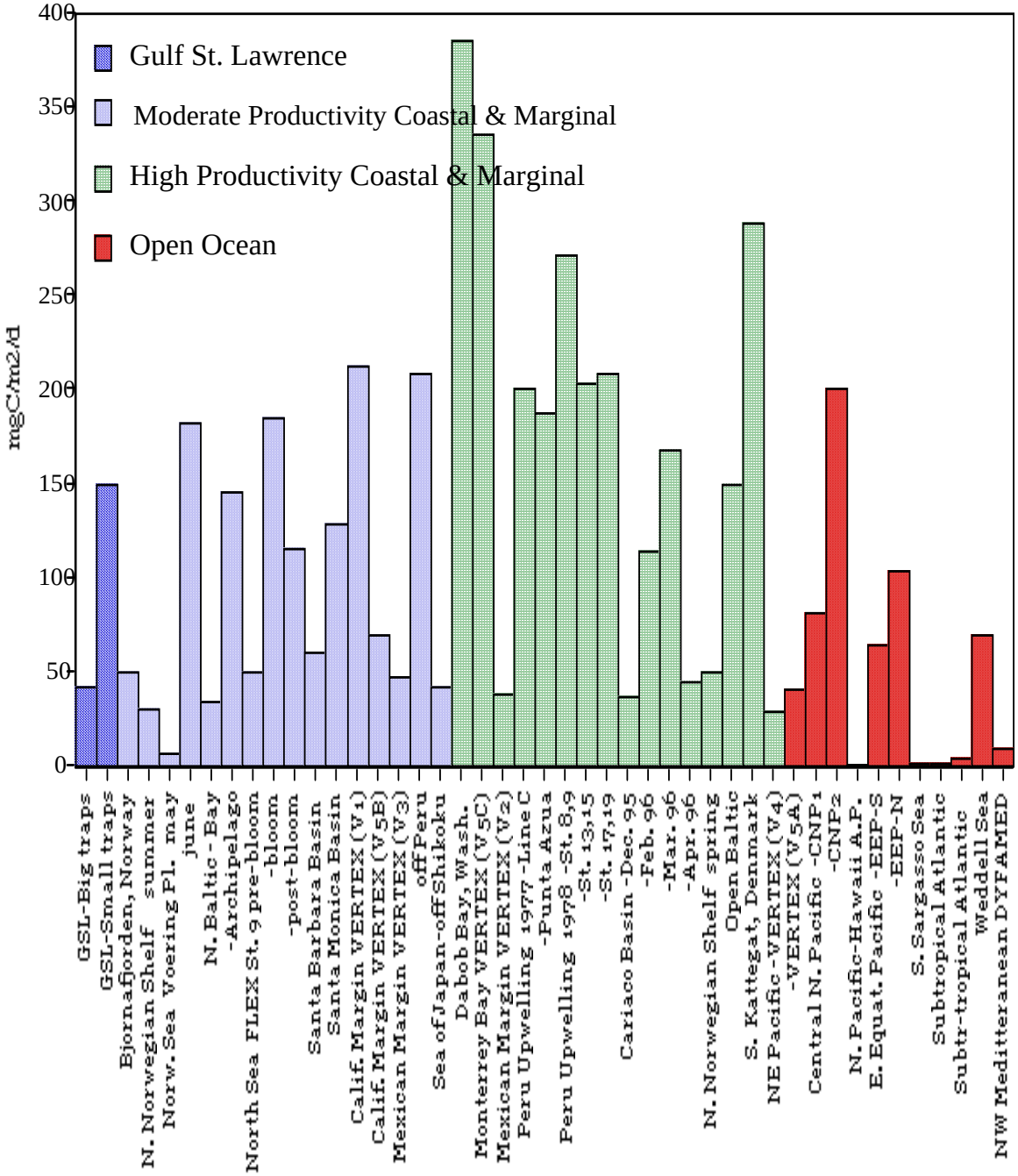

Figure. 17 Average POC fluxes in the Gulf of St. Lawrence (first two bars) together with POC fluxes from other locations. (See table 8)

Table 9: Estimation of the contribution of marine snow

Cruise / St.	Trap C Flux CHN	** Inorg C Flux	Total OrgC Flux	Total C Flux attributed	Marine Snow by diff.	Percentage of Total Carbon Flux (CHN)						
						Fecal	Phyto	Microzoo	Eggs+ Mesozoo	pollen	Total attributed	Marine Snow by diff.
	mgC/m2/d					%						
LargeTraps												
5 1B	19,6	0,3	19,3	5,4	14,2	11,4	10,5	3,2	0,9	0,0	27,5	**72,5**
5 6B	33,7	0,8	32,9	10,9	22,8	4,4	24,7	0,6	0,4	0,0	32,3	**67,7**
6 1B	47,0	1,4	45,6	18,2	28,8	10,6	20,0	1,1	0,0	4,1	38,8	**61,2**
6 6B	22,7	0,7	22,0	8,5	14,2	13,9	18,1	2,1	0,0	0,0	37,4	**62,6**
7 1B	16,8	1,2	15,6	26,6	-9,8	93,8	32,6	13,1	2,0	10,1	158,6	**-58,6**
7 5B	23,0	0,7	22,3	8,7	14,3	16,5	14,5	2,3	1,4	0,0	37,6	**62,4**
8 1B	67,0	3,3	63,7	13,7	53,3	5,2	9,2	0,1	1,0	0,0	20,4	**79,6**
8 4B	36,0	2,1	33,9	8,9	27,1	10,6	7,2	0,1	0,8	0,2	24,8	**75,2**
8 5B	10,0	0,6	9,4	7,5	2,5	50,7	18,0	0,0	0,0	0,0	74,9	**25,1**
9 1B	73,0	3,2	69,8	13,3	59,7	6,5	2,2	4,6	0,2	0,4	18,3	**81,7**
9 2B	78,0	2,5	75,5	20,0	58,0	10,7	7,1	2,5	1,2	0,8	25,6	**74,4**
9 3B	16,0	0,3	15,7	24,0	-8,0	42,4	34,2	44,4	21,1	6,1	150,3	**-50,3**
9 5B	122,0	4,1	117,9	21,7	100,3	6,9	4,5	0,7	2,0	0,3	17,7	**82,3**
Small Traps												
5 1s	166,9	2,8	164,1	18,5	148,4	2,9	5,5	0,5	0,6	0,0	11,1	**88,9**
5 4s	302,0	4,5	297,5	37,4	264,6	2,5	7,1	0,6	0,7	0,0	12,4	**87,6**
5 6s	78,2	4,6	73,6	317,0	-238,8	41,4	356,3	1,2	0,6	0,0	405,3	**-305,3**
6 1s	257,4	3,4	254,0	134,0	123,4	19,6	21,8	2,4	6,9	0,0	52,1	**47,9**
6 4s	220,4	3,9	216,5	152,1	68,3	28,4	36,4	1,7	0,4	0,3	69,0	**31,0**
6 6s	140,3	2,4	137,9	198,8	-58,5	22,2	84,0	14,8	3,8	15,1	141,7	**-41,7**
7 1s	194,6	2,8	191,8	120,7	73,9	37,5	20,6	2,5	0,0	0,0	62,0	**38,0**
7 4s	91,0	2,4	88,6	373,0	-282,0	81,7	298,5	9,4	17,6	0,0	409,8	**-309,8**
7 5s	148,9	5,8	143,1	115,2	33,7	61,6	6,1	4,4	1,1	0,3	77,3	**22,7**
8 1s	147,0	3,9	143,1	47,2	99,8	24,5	2,2	0,7	2,2	0,0	32,1	**67,9**
8 2s	124,0	4,0	120,0	79,4	44,6	41,1	19,7	0,0	0,0	0,0	64,0	**36,0**
8 2bs	124,0	4,3	119,7	65,2	58,8	29,7	16,3	0,0	3,1	0,0	52,5	**47,5**
8 4s	120,0	3,7	116,3	71,1	48,9	44,5	10,0	0,2	1,4	0,0	59,2	**40,8**
8 5s	83,0	2,7	80,3	28,2	54,8	23,1	7,7	0,0	0,0	0,0	34,0	**66,0**
9 1s	153,0	3,7	149,3	196,6	-43,6	65,9	42,4	4,6	9,8	3,4	128,5	**-28,5**
9 2s	88,0	1,5	86,5	257,2	-169,2	117,8	59,2	89,4	15,1	8,9	292,2	**-192,2**
9 4s	122,0	1,8	120,2	217,7	-95,7	95,3	35,7	10,4	31,8	3,7	178,4	**-78,4**
9 5s	184,0	6,2	177,8	173,7	10,3	74,8	8,5	2,1	2,1	3,5	94,4	**5,6**

** Total mass flux X Mean InorgC content in traps (Mucci et al., 2000)

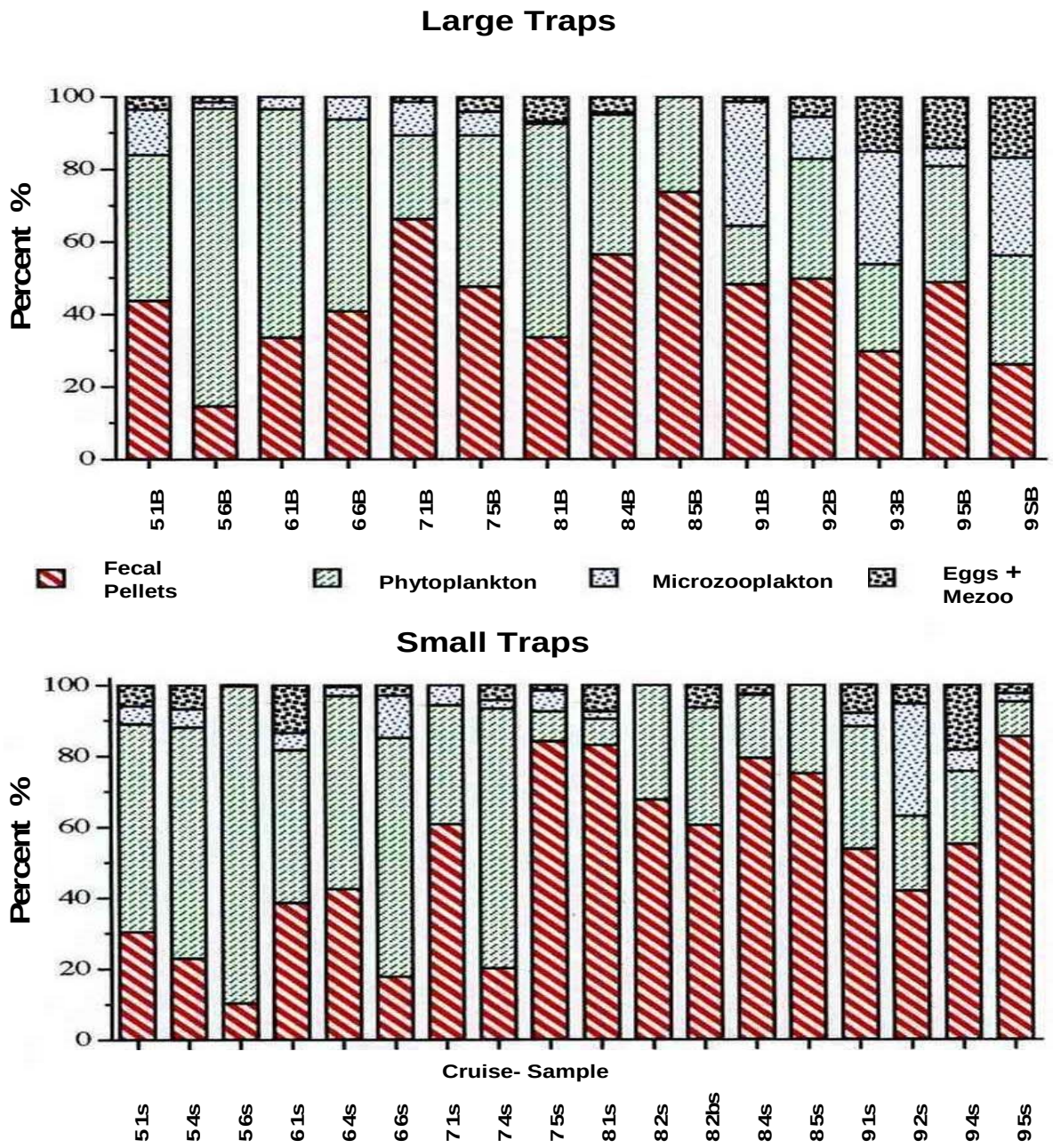

Figure 18. Relative contribution of vertical flux components to POC in large and small sediments traps

The subcomponents within each class (figs. 19, 20, y 21) display interesting patterns. Dinoflagellates are the most important phytoplankton carbon carriers in most of the samples (fig. 19), but are replaced by centric and pennate diatoms during April 1994 (cruise 8) and centric diatoms were also important during June 1994 (cruise 9). Among the fecal pellets (fig. 20), the compact rods dominate in all of the trap samples, except for the shallow Magdalene shelf site (St.4) in May-June 1993 (cruise 5), when loose rods and compact oval pellets made up 100% of the fecal carbon flux.

There is much more variability among sites and dates within a zooplankton class (fig. 21). Tintinnids are an important contributor, particularly during May-June, July and Nov-Dec 1993 (cruises 5, 6 and 7), as are other microzooplankton and small mesozooplankton and their detritus. Fish eggs tend to dominate in April 1994 (cruise 8), and their relatively rich carbon contents sporadically influence the zooplanktonic contribution to the total carbon flux.

3. 5 Discussion

After having generated the first estimates for the GSL of the contribution of the different particle types to the total organic carbon flux, the main question: "*What are the principal vectors of POC flux in the GSL?* can only be partially answered. There are two distinct fractions making up the particle flux. One is marine snow, whose contribution is assumed to be important, but for which it has not been possible to obtain a satisfactory estimate. The other fraction includes the particles with distinct cellular walls, peritrophic membranes or other boundaries and geometric forms viewed under the inverted microscope, for which carbon content and fluxes could be calculated (phytoplankton, fecal pellets, zooplankton). The latter can be examined in terms of their absolute fluxes, but interpretation has been based more on their relative contributions, as this offers more information on temporal changes and general trends.

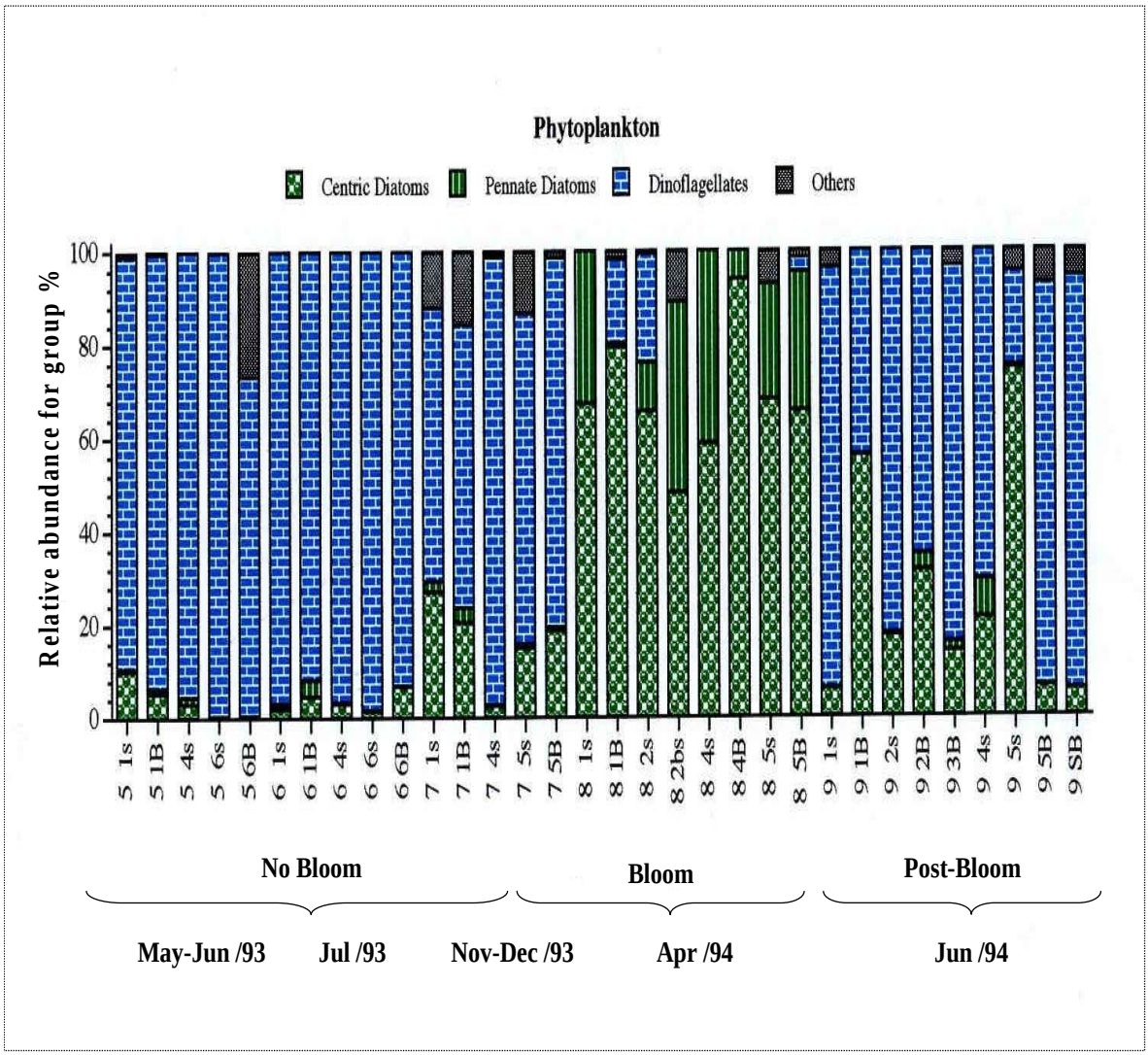

Figure 19. Relative carbon contribution to photosynthetic carbon flux by various taxa in the 1993-1994 cycle. Cruises 5-7 correspond to 1993 (May-June, July and Nov-Dec.) respectively and Cruises 8-9 correspond to 1994 (April and June) respectively. “B” indicates large traps and “s” small traps. The numbers identify the collection sites.

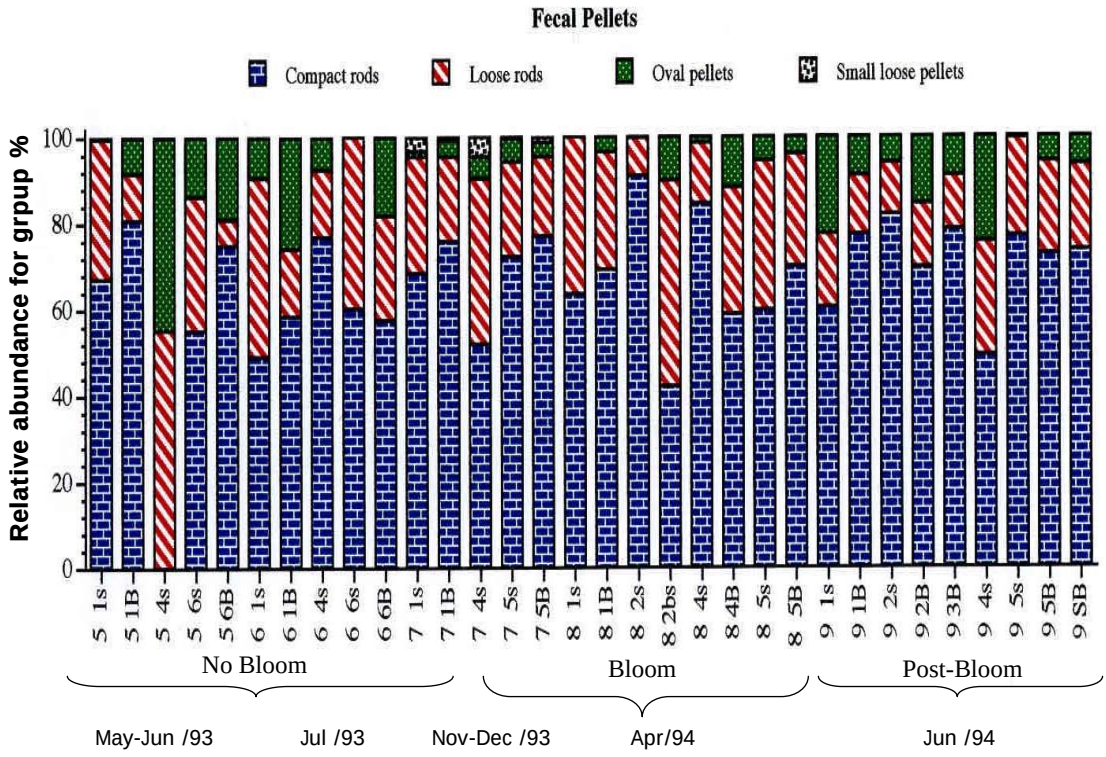

Figure 20. Relative carbon contribution to fecal flux by various types of fecal pellets during the cycle 1993-1994. The Cruises 5-7 correspond to 1993 (May-June, July and Nov-Dec.) respectively and Cruises 8–9 correspond to 1994 (April and June) respectively. “B” indicates large traps and “s” small traps. The numbers identify the collection sites.

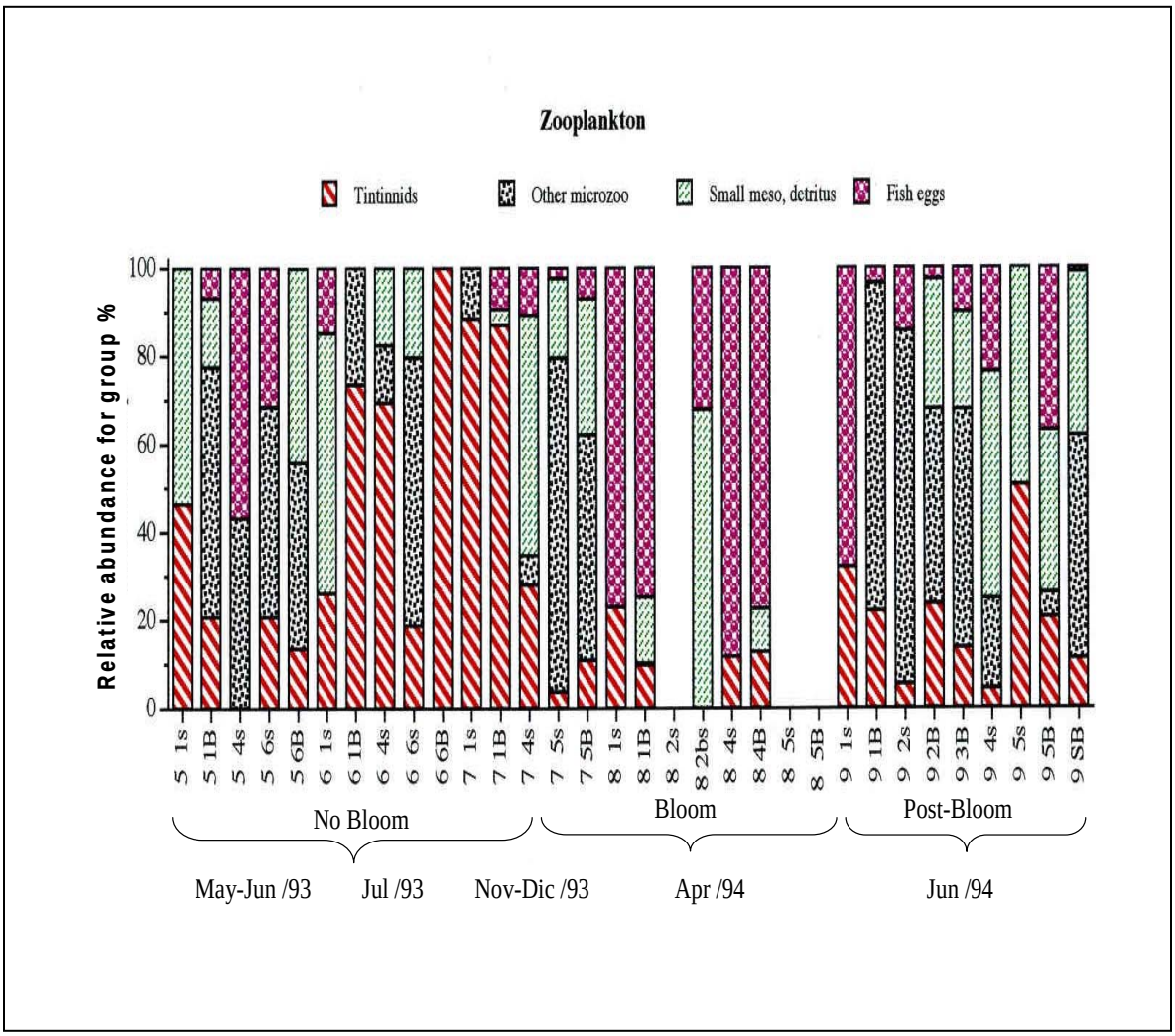

Figure 21. Relative carbon contribution to zooplanktonic flux by various components during the cycle 1993-1994. The Cruises 5-7 correspond to 1993 (May-June, July and Nov-Dec.) respectively and Cruises 8–9 correspond to 1994 (April and June) respectively. “B” indicates large traps and “s” small traps. The numbers identify the collection sites.

3. 5. 1 Absolute fluxes of carbon

The spectrum of carbon fluxes calculated for the 32 one-day drifting sediment traps (fig.16) reveals much heterogeneity, the variability associated with geographic influences confounded with that associated with temporal changes. The results reveal a

dominance of products of animal origin over that of plants in the trap samples. Fecal pellet carbon flux alone is greater than of phytoplankton in 60% of the samples and additionally there is the contribution of microzooplankton, zooplankton detritus and fish egg carbon. In 11 of the 22 samples where dinoflagellates occurred more than 50% of carbon derived from heterotrophic forms.

Eutrophic systems tend to export more carbon from the surface layers than oligotrophic systems (Eppley and Peterson, 1979; Hargrave, 1985; Pace *et al.*, 1987; Lalli and Parsons, 1993). The range of POC fluxes in the GSL is similar to that reported from some other continental margin areas (table 8, fig. 17), but the mean, particularly that of the more reliable large traps (42 mg m^{-2} d^{-1}) is still not very high, although considerably greater than that of some open ocean gyres. The flux measured in the GSL accounts for about 10% of the essentially mesotrophic estimated mean daily primary production of 411 mg m^{-2} d^{-1}, a percentage common in other continental margin areas and the ocean as a whole (Suess, 1980). The flux of fecal pellet carbon (1.5 –16 mg m^{-2} d^{-1}, is relatively high compared to fecal flux measured in other areas of similar primary production.

3. 5. 2 Relative carbon contributions of attributed components

Although there are obvious contributions by phytoplankton carbon (fig.19), heterotrophic components dominate the POC flux in the GSL. This is due to the strong contribution by fecal pellets (somewhat greater than phytoplankton), together with the generally smaller contribution of zooplankton and their body parts. Even within a phytoplankton class, there was an important contribution of non-photosynthetic dinoflagellates. In 42% of the trap samples that contained dinoflagellates, more than 50% of their flux was associated with heterotrophic genera.

The existence and succession of two distinct trophic regimes during the ice-free months in the GSL: autotrophic in late winter-spring; heterotrophic in summer and fall

(de-Lafontaine *et al*., 1991; Rivkin *et al.*, 1996; Savenkoff *et al*., 1996; Doyon *et al*., 2000; Roy *et al*., 2000; Savenkoff *et al*., 2000; Tian *et al*., 2000; Vezina *et al*., 2000) - is not clearly evident in the class comparisons of figure 18. Within these classes, however, the subcomponent carbon fluxes (as was the case for their numeric fluxes in Romero *et al.*, 2000) display patterns that better relate to the trophic changes observed in the water column (bloom, no-bloom, post-bloom).

Fecal matter was the principle vector for the vertical carbon flux in the GSL. Compact rods were the greatest contributors. Although the numeric fluxes of loose rods were similar to those of the compact forms (Romero *et al*., 2000), their lower densities (Urban *et al*., 1992; Dilling and Alldredge, 1993) and hence carbon: volume ratios (Silver and Gowing, 1991) account for their smaller contribution to the POC flux that those of compact rods.

Because of the dimensions of the most commonly occurring rods (50-109 µm in diameter), both types of pellets are considered to derive from the calanoid copepods, *Calanus finmarchicus* and *Calanus hyperboreus*, which dominated the water column during the sampling periods (Roy *et al*., 2000; Romero *et al*., 2000). Shifts in their relative contributions (e.g. the total absence of compact rods at St. 4 in June 1993, cruise 5) may be attributable to differences in food selection (Ayukai, 1990), reprocessing of pellets (Bathmann *et al*., 1990b; Noji, 1991), or their recycling in the surface layers (Vitassalo *et al*., 1999).

Oval pellets frequently contribute >10% of the total fecal carbon flux. Their origin may be multi-specific (Romero *et al*., 2000). Both their carbon fluxes and numeric fluxes were greater during non-bloom periods, with maximum values at St. 4 in May-Jun/93 (cruise 5, fig. 20). Small copepods such as *Temora longicornis* are more abundant at shallow shelf sites such as Sts. 4 and 5 (Roy *et al*., 2000) as opposed to the *Calanus sp* that dominate the deep Laurentian Channel.

The contribution of small loose pellets was minor and was only recorded at the end of autumn 1993 (cruise 7). The small copepods, *Oithona similis* and *Microcalanus pusillus*, were abundant in the water column at this time (Roy *et al.*, 2000) and are the likely source of these pellets.

Phytoplankton The phytoplankon contribution roughly followed the pattern of "No Bloom", "Bloom" noted for the GSL by Rivkin *et al.* (1996); Savenkoff *et al*. (1996); Vezina *et al*. (2000), as well as the numeric flux patterns of Romero *et al.* (2000), which added a summer 1994"Post-Bloom" situation.

Centric diatoms dominated the phytoplankton carbon flux (fig. 19.) during the April 1994 bloom period, while dinoflagellates dominated during no-bloom and post-bloom conditions. The greatest carbon contributors during the bloom period were the chain-forming genera *Thalassiosira* and *Chaetoceros* and the isolated centric diatom *Coscinodiscus*. Cells of *Fragilariopsis oceanica* and *Nitzschia* spp. contributed the most to the carbon flux of pennate diatoms, whose abundance was also appreciable during this period.

This last diatom group, and the dinoflagellates that were the greatest contributors to the phytoplankton carbon flux, partially reflect the high abundances and/or biomasses of the microphytoplankon present in the water column at the time of sampling. Lovejoy *et al*. (2000), for example, found that, in the surface layer, the pennate and centric diatoms - *Fragilariopsis oceanica*, and *Thalassiosira* spp.) and *Minidiscus* spp. and *Chaetoceros minimus*, dominated the autotrophs, while large dinoflagellates were represented by non-photosynthetic forms such as *Protoperidinium*. Three of the genus of diatoms (*Thalassiosira*, *Chaetoceros* and *Fragilariopsis*), also were the major vectors of phytoplankton carbon in the traps during the bloom period, while *Protoperidinium* spp. was a major contributor to the dinoflagellate carbon flux during the non- and post-bloom periods.

In a third of the traps, phytoplankton accounted for >50% of the total attributable carbon flux, but these large contributions were not from the bloom period,

but rather the no- and post-bloom samples when dinoflagellates dominated. If one looks within this group (fig. 22), most of the carbon is carried by autotrophic dinoflagellates, but a considerable portion is associated with non-photosynthetic genera (*Gymnodinium* and *Protoperidinium*). This heterophic contribution may explain the apparently high "phytoplankton" contribution during the periods of low primary production.

Zooplankton. Within this third most important class, the microzooplankton – tintinnids (particularly when their loricas were filled with larvae) plus "other" microzooplankton - were responsible for much of the flux of C of zooplanktonic origin (fig. 21). The importance of such living components, presumably part of the decomposing community (Shanks and Edmonson, 1990), has been noted at several sites in the NE Pacific by Silver and Gowing (1991).

Even if these small organisms can sometimes be captured by sediment traps as swimmers during their vertical migrations, Romero *et al.* (2000) point out that this is unlikely for the drifting traps used during this study, since no killing preservative was used and the traps were only deployed for 24 h. These "living" components are most probably integral elements of rapidly-settling marine aggregates.

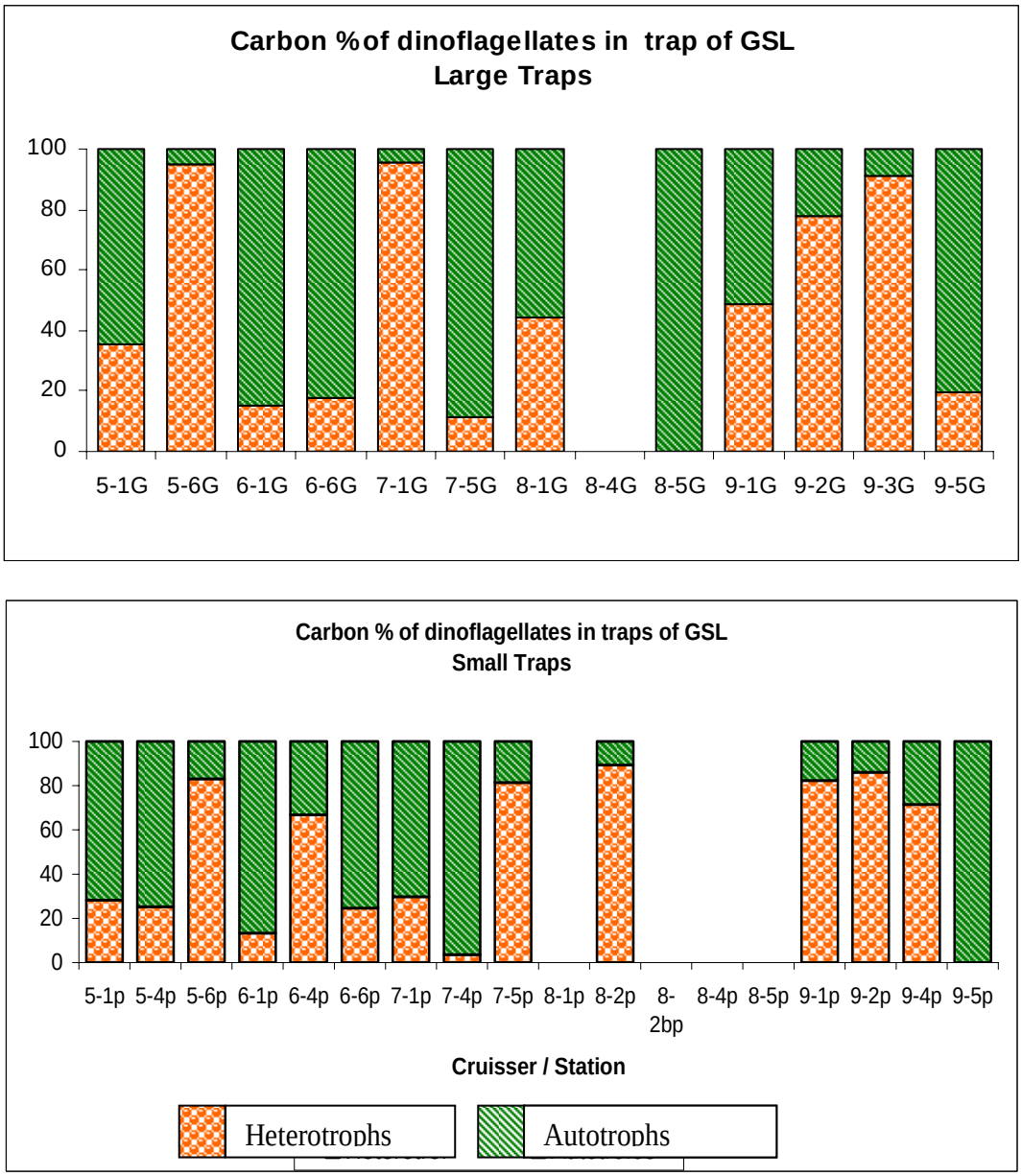

Figure 22. Carbon content attributed to dinoflagellates autotrophs and heterotrophs in large and small sediment trap

Small (<1 mm) mesozooplankton and detritus of mesozooplanktonic origin can also contribute greatly to the flux of animal carbon. Even though we tried to correct the disproportion between the flux of C and the numeric abundances (cf. Materials and Methods), the lack of clear trends among stations in fig. 21, is possibly attributed to the variable presence of only a few of these large particles rich in C. An important

contribution by eggs of fish was noted in the traps of the April 1994 bloom period, indicating the possible presence of spawning fish in the surface waters. The parallel distribution of fish eggs and larvae and the dominance of sand lace larvae in the NW Gulf and of sand lace and shinny to the south during spring have been pointed out by de-Lafontaine *et al.* (1984).

3. 5. 3 Importance of the contribution of heterotrophic carbon

The absence of massive fluxes of phytoplankton in the trap record from the GSL may simply be because such events were missed by the short-term deployments. They have been noted in other areas: waters coast and Kiel Bay (Smetacek *et al.*, 1978; Smetacek and Hendrikson, 1979; Smetacek, 1980, 1985); Bransfield Strait (in the Antarctic) (Bodungen, 1986); of Coast the North Europe (Peinert *et al*., 1986; Wassmann *et al.*, 1991, Passow and Wassmann 1994) in Canada (Tremblay *et al.*, 1989; Riebesell, 1991), in California (Alldredge and Gotschalk, 1989) in open ocean (Billet *et al.*, 1983; Buck and Chávez, 1994). In the GSL, neither the phytoplankton carbon flux during the spring bloom, nor the low abundances of phytoplankton pigments in the trap material (Roy *et al*., 2000) suggest that autotrophic carbon is the major component of the flux. In the estuarine portion of the Laurentian Channel, Colombo *et al*. (1996) also found that organic compounds of phytoplanktonic origin formed less than 20% of the organic matter. The relatively dense abundances of zooplankton in Gulf waters over much of the year (de-Lafontaine *et al.*, 1991) may contribute to the phenomenon.

In other parts of the world at similar latitudes, carbon from heterotrophs was also the principal characteristic of the vertical flux. Over the Voering Plateau in the Norwegian Sea, for example, copepod fecal pellets alone contributed almost 20% of the total POC flux. They dominated the flux off the coast of Denmark (Lundsgaard and Olesen, 1997), the northern Baltic Sea (Viitassalo *et al*., 1999). and were also important

in a Norwegian fjord (González *et al*., 1994). In the northern Humboldt Current, off Chile, they also constituted the bulk of the sedimenting material, accounting for 8-31% of the POC flux in free-drifting sediment traps (González *et al*., 2000).

2. 5. 4. Marine Snow and Other Uncertainties

Marine Snow.

The relative carbon contributions discussed previously assume that the greatest portion of the trap material is accounted for. Since the contribution of marine snow was not included, this is actually not the case. table 9 shows the marine snow contribution calculated (following Silver and Gowing, 1991) as the difference between the CHN-determined total C flux, (corrected for the small percentage of inorganic carbon), and the sum of the attributed carbon. The positive marine snow carbon fluxes resulting from this calculation ranged from 2. 5 to 100 mg C m^{-2} d^{-1} for the large traps (the small trap generally showing much higher fluxes), which contribute between 25 and 82% of the total POC flux. Such levels imply that this component is quite important. For comparison, in the NE Pacific, Silver and Gowing (1991) reported snow carbon fluxes of 10-200 mg C m^{-2} d^{-1} at the base of the photic zone. This accounted for 8-91% of the total carbon flux, with higher values associated with deeper traps, suggesting that some of this material is of refractive nature.

As mentioned previously, however, the negative snow carbon fluxes appearing in table 9 indicate that there are evidently considerable uncertainties in the entire procedure, whose cumulative effect all appear in this simple difference calculation. The CHN determinations for carbon content include an error of about ±2%, while the total mass fluxes vary by an average of ±14% (N. Silverberg, pers. comm.). These are not sufficient to cause the large negative results for marine snow. Instead, it is probably the microscopic sizing and conversion algorithm procedure that generates most of the uncertainty. Some of the factors that contribute to this are examined for various particle classes in the following paragraphs.

Uncertainties in the estimation of phytoplankton carbon.

To determine the volume of the phytoplankton cells, an estimate of their thickness must be made. Few microscopes allow the conversion of focal length to a precise measure of distance. Therefore, simple geometric forms end up being used to mimic the cell form and supply the third dimension needed to calculate cell volumes.

Many authors have used the volume to carbon relations obtained by Strathmann (1967) and their derivatives, for such calculations. This painstaking study directly measured the carbon contents of cells of different species whose volume had been estimated microscopically and linear correlation relationships discussed. However, Strathmann himself cautions his readers several times, mentioning, for example, that the Coulter Counter would be a better method to estimate cell volumes. He also declares that 'An estimate of the carbon in a diatom cell may be wrong by a factor of two...' (Strathmann 1967, p. 414). Others have noted that the thickness of diatom frustules and the size and chemical composition of phytoplankton cells vary during their life cycles so that the cellular: carbon ratio is not constant, Agbeti (1997, http:/www.indiana.edu/~diatom/biovol.dis)[5]. Fogg (1966), for example showed that the environment and the growth pattern determine the morphology and chemistry. Olivieri (1985) determined that preservative solutions could reduce cell size by as much as 77%. Sicko-Goad *et al*. (1977) mentioned that the cytology and plastic morphology of algal cells are affected by environmental conditions and that in the same natural population, the cells can be under different ambient conditions, thus complicating estimates of the carbon or chlorophyll contents.

Fecal pellet carbon.

The algorithms of Silver and Gowing (1991) used in this study to calculate the carbon associated with different fecal pellets (see Methods and Materials) appear to be

[5] (last consult 6 Sep/2005).

reasonable, having been based upon direct measures. They produce similar values to the direct measurements made upon selected fecal pellets from the GSL (Roy *et al*., 2000). The fact that the fecal carbon contribution in at least one case exceeded 100% of the total POC flux suggests that some imprecision remains. Some of the conversion factors appearing in the literature are much higher than those used in this study (table 10), indicating that considerable variation exists in their true carbon contents. This is probably related to their recent alimentary history (recent gut content of organisms). The nature of the fecal pellet contents of different zooplanktonic organisms reflects the variety in their diets. Examples of the analysis of copepod fecal pellet contents are presented in Turner and Anderson (1983); Bathmann *et al*. (1990); Urban *et al*. (1992); González *et al*. (1994b) and from the grazing of euphausid on ice algae (González *et al*., 1994a). Reports on feeding patterns and decomposition of fecal pellets have included the levels of photosynthetic pigments as well as carbon and nitrogen (Ayukai, 1990; Roy and Poulet, 1990; Head and Harris, 1992; Anderson, 1994; Thibault *et al*., 1999; Hayashi *et al*., 2001). Others have related feeding ecology with the rate of production, size, volumes and enzymatic activity of the feces (Buttler and Dam, 1994; Dagg, 1995; Thibault *et al*., 1999; Huskin *et al*., 2000).

Zooplankton.

In this study, only a single conversion factor (0.05 g $cm.^{-3}$) was used for all microzooplankton. Other considerations were signaled in the Methods and Materials section. In general, the corrections were introduced to reduce the even more excessive carbon fluxes that may have been the result from the uneven pipetting of a few carbon-rich large particles.

3. 5. 5 Importance of the marine snow contribution

Alldredge *et al*. (1993) and Kiørboe and Hansen (1993) have shown that much of the organic matrix of marine snow can be attributed to ‘transparent exopolymers’ (TEP)

Table 10. Divers factors of conversion carbon/volume in literature for fecal pellets

Direct measures of selected fecal pellets		
Source	mgC/mm^3	Comments
Strathmann (1967)	0.11	ofen uses though based upon diatoms
Ayukai and Hattori (1992)	0.027	after Knauer *et al* . (1979)
Dunbar and Berger (1981)	0.048	average of 8% organic matter (4% POC)
Alldredge and Cohen (1987)	0.113	average of various macrocrustaceans
Silver and Gowing (1991)	0.048 0.036 0.024	copepods and euphausids salps loose and amorphous
Gonzales *et al* . (1994)	0.057 0.042 0.016	copepods larvaceans euphausids
Butler and Dam (1994)	0.17 - 2.50	varies from late-early bloom conditions
Hansen *et al* . (1996)	0.28 0.39	newly egested pellets - diatom diet nanoflagellate diet
Lundsgaard and Olesen (1997)	0.061 - 0.30	copepods pellets in traps from Kattegat and in cultures

formed from the alteration of organic compounds exuded by diatoms in the ocean (Kiørbe and Hansen, 1993; Passow *et al.*, 1994), which act as a glue agglutinating fresh diatoms together with other particles in sinking aggregates (Alldredge and MacGillivary, 1991). Their abundance size and degree of colonization by bacteria can be highly variable (Passow and Alldredge, 1994; Mari and Kiørboe 1996). TEP particles hundreds of microns long and abundances of 28-500 ml^{-1} occur in coastal waters off California (Beers *et al.*, 1986). They are considered to be important to the aggregation and massive settling of phytoplankton blooms (Alldredge and Gotschalk, 1989; Passow *et al*., 1994; Alldredge *et al*., 1995; Waite *et al*., 1997; Ploug and Jørgensen, 1999; Ramaiah *et al*., 2001).

Organic glues with similar actions can also be produced by zooplankton, such as appendicularians (Alldredge, 1972; 1976), pteropods (Noji *et al.*, 1997) and other gelatinous organisms Their abundance size and degree of colonization by bacteria can be highly variable (Passow and Alldredge, 1994; Mari and Kiørboe, 1996). These substances can also be freed in the water as part of the digestive products of zooplankton organisms which do not produce distinct fecal pellets (e.g. tunicates, Pomeroy and Deibel, 1980). Ploug and Grossart (2000) show that dissolved organic carbon can make up 31% of the carbon associated with marine snow and that this make be underestimated if only POC is considered in the vertical flux.

The origin and the different types of marine snow aggregates sinking can be highly variable. Alldredge and Gotschalk (1989), have shown e. g. four “fresh” marine snow aggregates captured *in situ* at depth attainable by divers (diatom aggregates, fecal origin aggregates, abandoned larvaceans houses and miscellaneous aggregates). Alldredge (1998) following this study, estimed the carbon content from this four types of marine snow aggregates

Another attempt was made to evaluate the carbon content of the snow fraction using the approach of Alldredge (1998). In this approach, combined wet volumes were measured, dried, and the carbon contents were determined from the dry samples.

Relations between the volumes and the carbon content were derived from empirical equations for each one of the four types of marine snow aggregates present. For the GSL samples, the volume of marine snow aggregates was calculated using the estimates of the percentage of the low-power microscope field occupied by marine snow from Romero *et al*. (2000), assuming that these represent the area of a sphere projected on the plane of the microscope. The spherical volumes were then converted to µg C using the Alldredge (1998) empirical equation for miscellaneous aggregates ($C = 1.09\ V^{0.52}$). The results (table 11) are very much lower than those generated by the Silver and Gowing (1991) method. These low values are probably related to the reduced space occupied by the marine snow in the microscope samples compared to the fresh aggregates, as collected by Alldredge (1998). The material from the traps had likely exposed to partial degradation during settling and much physical alteration during sample processing. This could have resulted in much denser aggregates, for which an unknown correction factor would have to be applied to the Alldredge (1998) equations.

In the Gulf of St. Lawrence, assuming that the Silver and Gowing (1991) approach is closer to the truth, and that TEP is the predominant binding polysaccharide, than carbon of phytoplanktonic origin may be the most important element of the POC flux, depassing that of fecal pellets and microzooplankton. Electron microscopy could reveal if small nanophytoplankton cells and phytodetritus, too small to be detected easily with the inverted microscope, contributed significantly to the marine snow fraction. Organic chemical analysis of this fraction could also help in distinguishing the animal or algal dominance (products of animal origin dominate in the sinking matter found in the marine portion of the St. Lawrence Estuary. Colombo *et al.* (1996). Reducing the errors associated with the difference method will require a lot of care. One suggestion might be to refine the algorithms by limiting them to specific trophic systems and recent life history of each component. It would be useful to

Table 11. Uncertainties in the estimation of marine snow.

	FLUXES mgC/m2/d						% OF TOTAL POC FLUX	
					Marine Snow		Marine Snow	
Cruise / St.	Total C (CHN)	Inorg C	Total OrgC	Estimated OrgC	via Differ.	Alldredge	via Differ.	Alldredge
				LARGE TRAPS				
5 1B	19,6	0,3	19,3	5,40	14,2	0,10	72,5	0,5
5 6B	33,7	0,8	32,9	10,90	22,8	0,13	67,7	0,4
6 1B	47,0	1,4	45,6	18,20	28,8	0,40	61,2	0,9
6 6B	22,7	0,7	22,0	8,50	14,2	0,39	62,6	1,8
7 1B	16,8	1,2	15,6	26,60	-9,8	0,47	-58,6	3,0
7 5B	23,0	0,7	22,3	8,70	14,3	0,26	62,4	1,2
8 1B	67,0	3,3	63,7	13,70	53,3	0,53	79,6	0,8
8 4B	36,0	2,1	33,9	8,90	27,1	0,66	75,2	1,9
8 5B	10,0	0,6	9,4	7,50	2,5	0,38	25,1	4,1
9 1B	73,0	3,2	69,8	13,30	59,7	0,45	81,7	0,6
9 2B	78,0	2,5	75,5	20,00	58,0	1,33	74,4	1,8
9 3B	16,0	0,3	15,7	24,00	-8,0	0,82	-50,3	5,2
9 5B	122,0	4,1	117,9	21,70	100,3	1,95	82,3	1,7
				SMALL TRAPS				
5 1s	166,9	2,8	164,1	18,50	148,4	0,72	88,9	0,4
5 4s	302,0	4,5	297,5	37,40	264,6	6,43	87,6	2,2
5 6s	78,2	4,6	73,6	317,00	-238,8	2,10	-305,3	2,9
6 1s	257,4	3,4	254,0	134,00	123,4	3,93	47,9	1,5
6 4s	220,4	3,9	216,5	152,10	68,3	10,55	31,0	4,9
6 6s	140,3	2,4	137,9	198,80	-58,5	5,99	-41,7	4,3
7 1s	194,6	2,8	191,8	120,70	73,9	1,76	38,0	0,9
7 4s	91,0	2,4	88,6	373,00	-282,0	7,87	-309,8	8,9
7 5s	148,9	5,8	143,1	115,20	33,7	6,56	22,7	4,6
8 1s	147,0	3,9	143,1	47,20	99,8	1,79	67,9	1,3
8 2s	124,0	4,0	120,0	79,40	44,6	4,02	36,0	3,4
8 2bs	124,0	4,3	119,7	65,20	58,8	4,12	47,5	3,4
8 4s	120,0	3,7	116,3	71,10	48,9	5,94	40,8	5,1
8 5s	83,0	2,7	80,3	28,20	54,8	1,65	66,0	2,1
9 1s	153,0	3,7	149,3	196,60	-43,6	15,85	-28,5	10,6
9 2s	88,0	1,5	86,5	257,20	-169,2	1,47	-192,2	1,7
9 4s	122,0	1,8	120,2	217,70	-95,7	50,88	-78,4	42,3
9 5s	184,0	6,2	177,8	173,70	10,3	23,22	5,6	13,1

develop methods to physically separate the different flux components, using density gradients for example. These different components could be then be analyzed directly for their carbon content. This would constitute an improvement over the meticulous and time-consuming microscopic methods.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

CHAPTER IV General Discussion

Detailed results and discussions are provided in previous chapters of this study. In this section of the thesis some general observations and comments are presented.

The present study represents the first description and quantification of the various kinds of particles contributing to the vertical flux in the Gulf of St. Lawrence. The most common sinking particles in the Gulf of St. Lawrence (marine snow, zooplankton fecal pellets and skeletons of planktonic organisms) have all know from other areas (Honjo, 1997; Turner, 2002). Although there are many reports on the abundance of specific types of sedimenting particles in the literature, few researchers have attempted to include the entire range of particle types (except for Silver and Gowing, 1991).

Silver and Gowing (1991) have also reported the occurrence of microzooplankton, too small to be removed from trap samples, as a questionable part of the flux, organisms that may have entered the collecting cylinder as swimmers or during vertical migrations and then died in preservative solution. Their abundance in the Gulf sediment traps, despite the short collecting period and the lack of preservative solutions strongly suggests that such organisms are intimately associated with the bulk sedimenting material and must be considered as part of the natural flux.

Mineral fragments and seasonally abundant pollen grains represent the input from the continental areas that surround the Gulf.

Although too small to have been reliably counted under the inverted microscope, coccoliths, coccospheres or coccolith-enriched fecal pellets, commonly reported as seasonally significant components of the flux in oligotrophic open ocean environments (e. g. Cadée, 1985), were not observed in the Gulf of St. Lawrence.

Quantification of the contribution of nebulous marine snow particles remains a difficult task. In the present study, their contribution was estimated by the percentage of the total area that the aggregates occluded on the plane of the field of a dissecting microscope. This ranged between 2 and 65%, with an average of 15%. Given that the marine snow is three-dimensional, subject to continuous dispersal and re-aggregation, and occupies much space in the third dimension, the estimate is still tenuous. In aliquots sub-sampled for study at higher magnifications, however, marine snow was not evaluated: preparation of the sub samples for analysis results in dispersing the snow into particles too small to be quantified. The staining technique of Passow and Alldredge (1995), which provides a technique to visualize the transparent exopolymers (TEP) that characterizes marine snow derived from phytoplankton however, could well be useful in future studies for semi-quantitative analyses on snow-like material.

The present study has thus provided estimates of the quantitative flux of the major discernable components of particulate matter, whether these actually settled as individual particles or were associated with larger marine snow aggregates.

A comparison of these results with results from other ocean environments for which at least some similar data were available (see table 5) showed that the flux of diatom frustules fell between that reported for oligotrophic open ocean environments and that of high productivity coastal areas. The fluxes of fecal pellets in the Gulf of St. Lawrence, however, were among the highest reported.

An examination of the fluxes of fecal pellets of varying forms and diameter (see fig. 13, Chapter II) showed that, despite some variability, most of the pellets could be attributed to the copepod species that dominated the zooplankton in the water column. Similarly, the fluxes of different phytoplankton frustules observed in the trap samples reflected the composition of the (non-fragile) classes dominant in the water column at the time of sampling. These results suggests that, despite the uncertainties about the degree to which traps correctly sample, the drifting traps used in this study do provide a good record of the particles actually sedimenting through the water column.

Because of the sparse temporal coverage for many of the sampling sites, and the apparently strong bias towards over sampling by the cylinders of the small sediment traps, the most useful results turned out to be those on the relative contributions of the different particle types, rather than their absolute numerical fluxes.

This study shows that three trophic conditions, identified independently via direct collections obtained from the water column, were reflected in the contents of the sediment traps. A “bloom” period was characterized by the presence in the trap samples of pennate and centric diatoms, with fecal pellets identifiable zooplanktonic particles being less abundant. The “post-bloom” period was characterized by: the dominance of one species of centric diatom, with fewer dinoflagellates and microzooplancton. A third period “non-bloom” condition, where the phytoplankton abundance diminished notably and dinoflagellates were evident. Different types of fecal pellets, tintinnids and foraminifera also characterized this periode.

Another part of this study was concerned with evaluating the carbon flux attributable to various kinds of particles, and how their relative importance might change with the trophic conditions in the surface water. Absolute fluxes were estimated for the principal classes of particles by converting the microscopically determined long and short axes of particles, assuming a 3-dimensional geometry and a third axis, and applying published algorithms to convert volumes using the 3 axes to calculate an organic carbon content (table 6). The results (see figure 16) showed that, for the measurable particles:

(a) fecal pellets were a major component of the carbon flux.
(b) phytoplankton carbon rarely dominated the flux.
(c) microzooplankton and mesozooplankton products (molts, eggs) generally accounted for less carbon flux, but could occasionally become important
(d) variability was high among sites and between the large and small-diameter traps so that clear seasonal patterns could not be distinguished.

When the particle classes were examined in terms of their relative carbon contribution, (fig. 18) it was apparent that carbon of heterotrophic origin was more important than that of phytoplanktonic origin (particularly when a large portion of the latter often derived from heterotrophic dinoflagellates). There were some tendencies with respect to the different sampling cruises, e.g., relatively more phytoplankton carbon during cruises 5 (May-Jun), 6 (July) and 7 (Nov-Dec) in 1993, and more zooplankton carbon during the June 1994 cruise 9 (June-1994) (see fig. 18, Chapter III). The trends did not clearly follow the "non-bloom", "bloom" and post-bloom" trophic conditions described for the quantitative flux. (figs. 10, 11 and 12 Chapter II) Because of the small volumes and low carbon content of phytoplankton cells, their increased numbers during the April 1994 "bloom" condition were not enough to tip the balance of carbon flux in their direction. Indeed, the high contribution by fecal pellet carbon to the almost equally strong export flux during non-bloom conditions led Rivkin *et al*. (1996) to re-examine the conceptual model that assumed little interaction between the microbial loop and zooplankton.

Only when the broad classes of particles (phytoplankton, fecal pellets, zooplankton) were further subdivided into their relative contributions to their groups'_ carbon flux (see figures 19, 20 and 21, Chapter III) did their associations with the prevailing trophic conditions become clearer. The sharpest patterns were evidenced by the phytoplankton, where dominance shifted between diatoms and dinoflagellates. This is likely due to the fact that the carbon densities among the species were insufficient to overcome the great differences in their numerical fluxes.

Considering the labour-intensive nature of the carbon attribution procedure, it would appear that the simple counting of the particle types and the examination of their numeric fluxes provides a better index of the changing trophic conditions than does the estimation of their contribution to the organic carbon flux. This comment appears even more pertinent when our poor knowledge about the carbon contribution of the marine snow component is considered.

Marine snow carbon was determined by subtracting the sum of all the microscope-algorithm-based carbon contributions from the carbon flux independently determined from CHN analysis of another sample split. The results (see table 11, Chapter III) indicate that this component is generally the most important vector for carbon transport. A similar degree of importance was reported by Silver and Gowing (1991) for trap samples from a number of sites in the northeast Pacific. Other studies have been attempted to estimate this dominant component of the flux. *(*Bishop *et al*., 1977, 1978).

Table 11 (Chapter, III), however, shows some disturbing negative values. These mean that some of the "attributed" carbon fluxes must be overestimated and raises doubts about all of the particle class calculations. The difference method essentially groups all of the experimental errors within the marine snow carbon flux estimate. The methodological uncertainties include the following:-slight biases during sample subdivision, dilution and sedimentation chamber procedures due to large differences in settling velocities among particles; - errors associated with the simplification of particle form and estimation of the third dimension; - use of algorithms that assume average carbon densities for all particles of the same class; and the large multiplication factors applied when converting data from small splits to trap fluxes in terms of m^2/day.

The algorithms used have been based upon a small number of studies in which the samples of the particle class in question were physically separated for independent density and carbon analysis. It is possible that natural populations of particles display considerable variation in these parameters. If this is true, then it would be best to establish separation procedures which would permit the direct evaluation of the carbon content of at least some of the major particle classes.

An alternative procedure is presented in the annex to this thesis, based upon the physical separation of different classes of particles based upon their settling velocities. Once separated they can be analyzed independently (by CHN analyzer, for example) for their carbon contents. While the results of these experiments on trap samples from Bahía Concepción, B.C.S. and from the GSL, are not conclusive, such a method is very much

simpler, less time consuming and probably more accurate than algorithmically converting dimensions measured under a microscope.

General Summary and Conclusions

1) Based upon the average POC flux (42 mg Cm^{-2} d^{-1}) and the mean rate of primary production (411 mg C m^{-2} d^{-1}), the Gulf of St. Lawrence regime varies from low (oligotrophic) to moderately (mesotrophic) productive

2) Because of the limited amount of station data, spatial and temporal variations are confounded. The best time series was obtained at Station 1 (Mont-Louis) where the total mass and carbon fluxes remain high even during the winter months with ice cover.

3) The present study provides the first quantitative description of the various types of particles that contribute to the flux of sedimenting material in the Gulf of St. Lawrence. These consist of a heterogeneous mixture of particles of different types, size, consistency, color and origin. They include varying abundances of marine snow aggregates, fecal pellets, phytoplankton, microzooplankton, zooplankton detritus, mineral grains and pollen.

4) Despite the sampling limitations, the numeric fluxes (# of particles/m^2/d) show seasonal changes that correspond to the two trophic regimes ("bloom" and "non-bloom") identified from studies carried out simultaneously in the upper water column. In addition, the trap results point out an intermediate situation, identified in this study as "post-bloom".

5) In terms of the flux of organic carbon, the principal vectors of the settling flux were, in order of importance, fecal pellets, phytoplankton and zooplankton.

6) The contribution to the carbon flux of components of heterotrophic origin appears to dominate over that of autotrophic phytoplankton in this coastal environment.

7) The contribution of marine snow was difficult to evaluate. One attempt was based upon the proportion of the microscope field that was occupied by the snow aggregates. These results show that their two-dimensional projected area was relatively unimportant.

8) On the other hand, in terms of their contribution to the carbon flux, obtained by the difference between the total carbon (CHN) flux and the sum of that all of the other components (microscope-determined dimensions and algorithms for their carbon content) marine snow is a very important vector for carbon sedimentation (generally between 23 and 89% of the total flux).

9) The estimated marine snow carbon contributions, however, include all of the errors involved in the estimates of all of the other components. The fact that this sometimes resulted in negative flux values makes it difficult to accept the snow carbon contributions as truly accurate. However, a simple laboratory experiment indicates that the physical separation of the most important particle classes and the direct determination of their carbon content might offer more rapid and more certain estimates of their contributions to the overall carbon flux.

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APPENDDIX

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USE OF SETTLING VELOCITY FOR THE SEPARATION OF PARTICLES IN SAMPLES FROM THE GULF OF ST. LAWRENCE (CANADA)

One of the difficulties in working with material collected by sediment traps is the physical separation of the collected particles, particularly if marine snow aggregates are included in the mixed collection. Such aggregates, semitransparent and adhesive, tend to agglutinate the rest of the particles, making difficult their separation, identification or whatever kind of measurement, counting or analysis that requires determination, since marine snow itself is one of the constituents of the flux of settling particles. One of the most difficult analyses to achieve is the determination of the carbon fluxes each contributes to the total POC flux.

Trying to find a methodology that would permit the physical separation of these particles, in order to directly measure their carbon contents, instead of using indirect methods much more difficult and laborious to carry out, such as microscopic measurements, a separation method was tested on particles from sediment trap samples. This was carried out as a research stay undertaken with samples taken in Conception Bay, which contained abundant material to provide replicates.

Brief Description of the Procedure

- After a number of tests using different settling media (sugar solution, layers of salt and sugar solution, Percoll and various concentrations of salt solution) it was found that the best solution for the separation by sedimentation of the particles was a saturated salt solution.

- A preparation was made of 18 liters of demineralized water, saturated with salt (NaCl), so as to use the same water of the same density (d =1.19 g/cm^3), throughout the experiment.

- 350 grams of NaCl were dissolved for each liter of hot demineralized water and allowed to cool at ambient temperature (22-24 °C).

- The saturated solution was introduced into a 1-liter glass cylinder.

- A trap sample was carefully emptied into the cylinder of saline solution, washing the walls of the sample tube with the same solution.

- Tests were made to determine the optimal sedimentation period for separation of the particles. Over a range of 4-13 minutes, it was found that 4 minutes was enough for the heaviest particles to reach the bottom and for the rest of the material.

- When enough material used was used (similar to that recovered by time-series traps of several days of collection), a good separation of particles was achieved, easily seen in the settling cylinder.

- The particles extracted from each zone were then observed under the stereoscope and the following percentage distribution was obtained:

Zone I	95 % marine snow (very fine aggregates) 5 % Mix of centric and pennate diatoms (single cells or in chain) and fine mineral grains.
Zone II	60 % marine snow 30 % centric and pennate diatoms (single cells or in chain) 8 % Tintinnids and very fine mineral grain. 2 % Small fragments of loosely compacted fecal pellets.
Zone III	90 % loose and compact fecal pellets, whole or fragments of various diameters. 8 % Tintinnids

2 % Mix of small centric diatoms in chain, a few pennate, Globigerina shells, mineral grains, zooplankton molts and small gastropods.

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The same technique was applied to selected samples from the Gulf of St. Lawrence.

Observations of the separation procedure of samples from GSL

An initial trap sample was carefully emptied into the cylinder of saline solution, washing the walls of the sample tube with the same solution. The previously determined optimal time (4 minutes) was waited, but only 2 zones were formed, a semi-transparent layer that occupied most of the volume of the cylinder, and the second almost the bottom of the cylinder.

The separated material was recovered from each zone for observation under the stereoscope. The first zone contained a mixture of marine snow, diatoms and very small tintinnids. The second zone contained fecal pellets of different form, foraminifera shells, some mineral grains and molts of zooplankton organisms.

A second dilution was made to try to purify the first zone, but the marine snow and diatoms were still found throughout the length of the column, without observing any separation under the stereoscope. Of the samples, which had been considered for analysis, those containing the most material (since in general all of the 24 hour sediment trap samples contained very little material for treatment) were selected, and processed by repeating each of the previous stages.

Despite having slightly more material, we again did not observe the formation of three different zones after the optimal 4 minutes, as had been the case for the procedure developed with the samples from Conception Bay. Again, only 2 zones were formed, with identical characteristics as the first sample. Zone I occupied most of the cylinder volume

and showed marine snow mixed with diatoms and some small tintinnids. Zone II contained fecal pellets, shells, some mineral grains and zooplankton molts.

The remaining 4 samples (6 in total) behaved the same way as the first 2 when the separations were carried out. Again only 2 zones formed, a layer with the fastest settling and dark colored particles at the bottom of the cylinder, and the first zone, semi-transparent corresponded to the largest volume of the cylinder.

We then proceeded to filter the material from each of the two zones formed in each of the 6 samples, onto dried, pre-weighed 25 mm diameter GF/F fiberglass filters, to obtain the dry weight of the filtered material. The filters were sent for CHN determination at the University of California, Santa Barbara USA laboratory.

Results

The results are presented in table 1. The carbon contents of the material from the 6 samples physically separated by sedimentation are compared with the contents of four of the drifting traps deployed in the GSL, previously determined using the procedures of the thesis (using microscopic dimensions, volume estimates and C organic content algorithms). St. "S", a sample from the continental slope off Nova Scotia included because there was a fair amount of material for the separation technique, was not analyzed for individual carbon contributions in the thesis.

The values marked in blue tell us that despite the small number of samples analyzed, it is possible to observe similarities in the carbon levels of the marine snow, phytoplankton and microzooplankton between the two methods, as well as close values for the carbon content of fecal pellets and mesozooplankton.

Even though there was little material available from splits of 24-hour traps and possible effects due to the long period of storage in preservative, this test with a few samples from the GSL, already yielded some interesting results.

Table 1. Sampling date and trap type (P = small) (G = large); type of particle (fecal, shell, mesozooplankton) (marine snow, phytoplankton, microzooplankton), weight in µg, carbon content in µgC, the fraction they represent of -- the total sample weight, the total carbon and organic carbon – compared to the values estimated in the work of the thesis (carbon assigned to specific types measured under the microscope) in the Gulf of St. Lawrence. *Corrected for average C inorganic in GSL trap samples.

Date	# Station trap	Kinds of particles	Experimento					C. Org. Thesis	
			Wt. (ug)	C µg	Fracc'n Total Wt.	Fracc'n Total Carbon	Fracc'n Org. Carbon	Sum	only fecal or snow
16-Jun-94	St. 4P	Fecal, conchas, mesozoo	760	98,0	0,0116	0,219	0,210	1,271	0,953
22-Jun-94	St. 2G	Fecal, conchas, mesozoo	3830	169,6	0,0118	0,181	0,174	0,119	0,107
18-Jun-94	St. 5G	Fecal, conchas, mesozoo	1750	120,3	0,0117	0,173	0,166	0,089	0,069
01-Jun-93	St. 4P	Fecal, conchas, mesozoo	3950	128,6	0,0114	0,202	0,194	0,032	0,025
28-Jun-94	St. SG	Fecal, conchas, mesozoo	4240	221,9	0,0241	0,494	0,475		
28-Nov-93	St. 4P	Fecal, conchas, mesozoo	2560	135,3	0,0162	0,297	0,285	0,993	0,817
16-Jun-94	St. 4P	Nieve marina, fito, microzoo	7660	349,5	0,0415	0,781	0,750	-0,324	-0,784
22-Jun-94	St. 2G	Nieve marina, fito, microzoo	10570	768,2	0,0533	0,819	0,787	0,840	0,744
18-Jun-94	St. 5G	Nieve marina, fito, microzoo	8510	574,3	0,0560	0,827	0,794	0,868	0,823
01-Jun-93	St. 4P	Nieve marina, fito, microzoo	7350	507,9	0,0449	0,798	0,767	0,953	0,876
28-Jun-94	St. SG	Nieve marina, fito, microzoo	4980	227,5	0,0247	0,506	0,486		
28-Nov-93	St. 4P	Nieve marina, fito, microzoo	5810	320,3	0,0383	0,703	0,676	0,174	-3,098

In addition, in spite of the fact that the separation of the GSL samples was not as good as that of the original experiments on more abundant, much fresher material from Conception Bay, wherein it was possible to isolate 3 zones, one of which contained 95% marine snow, the simple fact that with a few days of work in the laboratory one can arrive at results similar to those obtained from almost a year's observations under the microscope and more time in laborious calculations and data analysis, represents substantial progress.

The observations and results of this first attempt to physically separate particles captured by sediment traps shows us that separation is possible and motivates us to continue perfecting a technique that would permit us an enormous saving of time and effort when estimating the carbon content that different particles contribute to the vertical flux