

UNIVERSITÉ DU QUÉBEC À RIMOUSKI

**CYCLE ANNUEL DU FLUX VERTICAL DE
PARTICULES DANS LE GOLFE DU SAINT-
LAURENT : LE RÔLE DES ORGANISMES
PLANCTONIQUES**

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AVANT-PROPOS

Ce mémoire traite du flux vertical de matière organique particulaire à deux profondeurs à la marge du chenal Laurentien dans le golfe du Saint-Laurent. Il présente une série annuelle complète du flux vertical de matière organique particulaire ainsi que l'identification du matériel trouvé dans les échantillons. L'échantillonnage a été effectué au moyen de pièges à particules de l'Institut des sciences de la mer de Rimouski qui ont été mouillés et récupérés lors de missions d'échantillonnage menées par l'Institut Maurice-Lamontagne (IML). Cette étude vise l'amélioration des connaissances sur les flux verticaux dans le golfe du Saint-Laurent, leur lien avec les conditions océanographiques ainsi qu'un suivi de l'évolution des flux verticaux dans un contexte de changement climatique. Cette étude vise également l'amélioration des connaissances en matière d'écologie planctonique dans le golfe du Saint-Laurent.

Ce mémoire se compose d'un résumé en français et en anglais, d'une introduction générale en français, d'un chapitre central sous la forme d'un article scientifique en anglais et d'une conclusion générale en français. Les résultats de cette étude ont été présentés en 2016 sous forme d'affiche lors de l'Assemblée générale annuelle de Québec-Océan et en 2017 sous forme de présentation orale au « 14th International Estuarine Biogeochemistry Symposium » ainsi qu'au colloque de vulgarisation scientifique de l'Université du Québec à Rimouski « La nature dans tous ses états ».

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RÉSUMÉ

Le cycle océanique du carbone est un sujet de recherche actif depuis plusieurs décennies. Les études menées ont notamment comme finalité d'évaluer la quantité de carbone que les océans peuvent emmagasiner et l'impact des activités anthropiques sur le cycle du carbone. Une façon d'évaluer l'intensité des processus concernés par ce cycle est de mesurer les flux verticaux de carbone. Dans le golfe du Saint-Laurent (GSL), ceux-ci ont déjà été mesurés à plusieurs stations lors du programme canadien du « Joint Global Ocean Flux Study » (JGOFS) qui a occasionné une vaste campagne d'échantillonnage de 1992 à 1994. Cependant, aucune série annuelle complète n'a été obtenue pour aucune des stations échantillonnées. Dans la présente étude, des pièges à particules ont été déployés dans le chenal Laurentien au nord du détroit de Cabot, à 34 m et à 100 m de profondeur, pendant une année complète. Ces nouvelles mesures viennent compléter les connaissances sur les flux verticaux de carbone et l'écosystème du GSL. Le flux annuel de carbone organique particulaire (COP) observé dans cette étude était très faible, $1.06 \text{ g m}^{-2} \text{ an}^{-1}$ à 100 m, ce qui est consistant avec le caractère océanique de la station échantillonnée. Lors de la floraison printanière, les flux étaient nettement plus élevés que le reste de l'année et composés majoritairement de diatomées à 34 m (59% de la masse carbonée) ou de pelotes fécales de zooplancton à 100 m (63% de la masse carbonée). La composition taxonomique du flux a fortement varié au long de l'année et montre une succession écologique importante des organismes planctoniques. Les flux verticaux de COP mesurés étaient 3-5 fois moins importants durant la floraison printanière et jusqu'à 76 fois moins le reste de l'année que durant la campagne JGOFS-Canada qui a eu lieu principalement dans des secteurs plus productifs à l'ouest, au nord et au sud du Golfe. Le caractère océanique de la station échantillonnée est probablement responsable de cette différence. En plus de quantifier les flux verticaux, cette étude a permis de caractériser l'importance de nombreux organismes planctoniques dans le GSL, dont certains sont encore nettement sous-étudiés. Des études ultérieures devront tenir compte de ces organismes afin de mieux comprendre le fonctionnement de l'écosystème du GSL.

ABSTRACT

The oceanic carbon cycle has been an active research topic for several decades. The aim of these studies is notably to estimate the amount of carbon that oceans can store and the impact of human activities on the cycle. One way to evaluate the intensity of the processes involved in this cycle is to measure vertical carbon fluxes. In the Gulf of St. Lawrence (GSL), these have already been measured at several stations during the Joint Global Ocean Flux Study (JGOFS) program, which resulted in a large sampling campaign from 1992 to 1994. However, no complete annual series was obtained for any of the sampled stations. In this study, particle sediment traps were deployed in the Laurentian Channel north of Cabot Strait at 34 m and 100 m depth for a full year. These new measurements complement the knowledge on vertical carbon fluxes and the GSL ecosystem. The annual flux of particulate organic carbon (POC) observed in this study was very low, $1.06 \text{ g C m}^{-2} \text{ y}^{-1}$ at 100 m, which is consistent with the oceanic character of the station sampled. During the spring bloom, the fluxes were significantly higher than the rest of the year and composed mainly of diatoms at 34 m (59% of the carbon mass) or fecal pellets of zooplankton at 100 m (63% of the carbon mass). The taxonomic composition of the flux varied strongly throughout the year and showed a significant ecological succession of planktonic organisms. The vertical fluxes measured in this study were very low: 3-5 times less during the spring bloom and up to 76 less the rest of the year than during the Canadian JGOFS campaign, which was carried out mainly in more productive sectors in the west, north and south of the gulf. The oceanic character of the sampled station is most likely responsible for this difference. In addition to quantifying vertical fluxes, this study has characterized the importance of many planktonic organisms in the GSL, some of which are still significantly under-researched. Future studies will need to consider these organisms to better understand the functioning of the GSL ecosystem.

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1. INTRODUCTION GÉNÉRALE

1.1. Les pompes océaniques du carbone

Il est bien connu aujourd'hui que les océans occupent une place de grande importance dans le cycle biogéochimique du carbone. Trois grands processus sont généralement reconnus dans la partie océanique de ce cycle : la pompe de solubilité, la pompe du carbone organique et la pompe des carbonates (Volk et Hoffert, 1985 ; Heinze *et al.*, 1991). Ensemble, ces processus contribuent à tamponner l'augmentation de CO₂ atmosphérique due aux émissions anthropiques (Denman *et al.*, 2007 ; Le Quéré *et al.*, 2016). On estime que l'océan a absorbé près d'un tiers du CO₂ d'origine anthropique depuis le début de l'anthropocène (Sabine *et al.*, 2004). Comme on sait que les changements climatiques ont des effets sur le cycle global du carbone (Riebesell *et al.*, 2009), il est important d'étudier les phénomènes sous-jacents afin de tenter de comprendre les enjeux à venir.

La pompe de solubilité est un processus physique. Il consiste en un échange de dioxyde de carbone gazeux à l'interface atmosphère-océan du milieu le plus concentré vers le milieu le moins concentré. La solubilité du CO₂ croît avec la baisse de température et salinité (Heinze *et al.*, 1991). Donc les eaux plus douces et froides (eaux côtières et de haute latitude) emmagasinent une plus grande quantité de carbone via ce processus que les eaux chaudes et salées (eaux océaniques et tropicales). Ce processus rend le carbone atmosphérique disponible dans l'eau pour les deux processus biologiques suivants : la pompe du carbone organique et la pompe des carbonates.

La pompe du carbone organique comprend l'ensemble des phénomènes liés à la fixation, la transformation et au relargage de carbone organique dans l'eau, sous forme dissoute ou particulaire (Ducklow *et al.*, 2001 ; Pörtner *et al.*, 2014). Ce processus peut être responsable d'un enfouissement net de carbone

dans la colonne d'eau. Du CO₂ dissous est fixé dans la zone euphotique par la photosynthèse du phytoplancton. Une partie du phytoplancton sédimente directement sous la forme de cellules intactes ou sénescents. Une autre partie est consommée par le zooplancton et entre ainsi dans le réseau trophique. À partir de là, cette production peut éventuellement sédimer sous forme de pelotes fécales ou de débris planctoniques. En sédimentant et en présence de substances exopolymériques favorisant ce processus, le carbone fécal, le phytoplancton sénescents et d'autres débris peuvent s'agréger et former de la neige marine (Turner, 2015). Celle-ci a généralement une vitesse de chute plus importante que les particules qui la composent (De La Rocha et Passow, 2007). La formation de neige marine est donc un processus accélérant l'enfouissement de carbone. Un processus atténuant l'enfouissement est la reminéralisation bactérienne de la matière organique (Buesseler et Boyd, 2009). Celle-ci a généralement lieu sur l'ensemble de la colonne d'eau. Un autre destin possible pour le carbone issu de la production primaire est de finir sous forme de carbone organique dissous (COD). Le COD est formé principalement par la décomposition microbienne (Turner, 2015). On estime que l'océan contient, en termes de masse, 38 fois plus de COD que de COP (Denman *et al.*, 2007). Ceci s'explique notamment par la durée de vie nettement plus importante du COD par rapport au COP (Legendre et Gosselin, 1989). Le COD est cependant moins important pour l'enfouissement du carbone dans la colonne d'eau étant donné qu'il ne coule pas. Sa répartition dans l'océan est donc dépendante de processus d'advections. Ceux-ci ont lieu sur une échelle de temps nettement supérieure à celle de l'export du COP qui se fait sur un an au plus (Legendre et Gosselin, 1989). Généralement, environ 1% du carbone organique généré en surface atteint le fond de l'océan (Ducklow *et al.*, 2001). La fraction de la production totale qui est exportée hors de la zone euphotique est généralement plus importante dans les eaux froides et productives (Laws *et al.*, 2000).

La pompe des carbonates est un processus qui fixe du carbone inorganique via la production de structures calcaires par certains organismes (p. ex. ptéropodes, foraminifères, coccolithophores ; Heinze *et al.*, 1991). Comme le phénomène libère du dioxyde de carbone dissous, on le nomme également « pompe inverse ». La calcification a généralement lieu dans les eaux de surface tandis que la dissolution des parties dures se passe dans l'océan profond. Ce processus libère donc du CO₂ dissous là où la pompe du carbone organique en fixe.

1.2. Les programmes de recherche et les avancées majeures

L'étude du cycle du carbone a déjà été appuyée par de nombreux programmes nationaux et internationaux depuis le milieu des années 1980 à aujourd'hui. Le plus ambitieux était sans nul doute le « Joint Global Ocean Flux Study » (JGOFS, 1987-2003). Ce dernier avait pour but de comprendre les processus contrôlant régionalement et globalement les flux de carbone entre l'atmosphère, la surface de l'océan et l'océan profond (Scientific Committee on Oceanic Research, 1990), notamment dans le golfe du Saint-Laurent (GSL; Roy *et al.*, 2000b). Ce programme s'est aussi intéressé à la sensibilité des flux aux changements climatiques. Il a permis de quantifier les flux aux interfaces et d'identifier les zones du globe où ces flux sont les plus importants. L'intensité de la pompe biologique (la quantité de flux de matière) a été mesurée dans des régions clés, permettant d'estimer son efficacité (le rapport entre le carbone exporté en profondeur et celui produit dans la couche de surface) moyenne à moins de 3% (pour des périodes excédant 1000 ans). La capacité d'absorption des océans a pu être estimée, représentant entre un tiers et la moitié du carbone anthropogénique. Les résultats de l'étude ont suggéré que le changement climatique diminuerait cette capacité d'absorption dans l'avenir (International Geosphere-Biosphere Program, 2001). Le « Vertical Transport and Exchange » (VERTEX, 1979-1989) était un programme qui a eu lieu dans le Pacifique Nord-Est (Martin *et al.*, 1989). Ce programme avait pour buts de quantifier la

matière et les flux dans les 2000 m supérieurs de l'océan, estimer les temps de résidence et comprendre les mécanismes de transport (Martin *et al.*, 1983). Ce programme a mené au constat que le flux de carbone décroît avec la profondeur dans les océans, sur des échelles de plusieurs centaines de mètres. Cette décroissance a aussi pu être quantifiée au moyen d'une relation mathématique (voir Martin *et al.*, 1987). Le « Vertical Transport In the Global Ocean » (VERTIGO, 2004-2005) était une étude multidisciplinaire qui a visé à mieux comprendre les mécanismes régulant la magnitude et l'efficacité du transport de particules dans la zone mésopélagique (Buesseler *et al.*, 2008). Cette étude s'est intéressée à deux stations contrastées dans le Pacifique Nord, montrant que l'efficacité du transport du carbone en profondeur pouvait varier fortement entre les régions et remettant en question l'universalité du modèle de Martin *et al.* (1987) à travers les océans du globe (Buesseler *et al.*, 2007b ; Buesseler et Lampitt, 2008). Les conclusions de l'étude ont permis d'identifier les principaux facteurs responsables de la variation d'efficacité du transport de carbone : la dégradation hétérotrophe, le transport actif par le zooplancton et l'advection latérale de particules.

Ces différentes initiatives ont donc permis de comprendre les mécanismes impliqués dans le cycle du carbone océanique, notamment la pompe biologique ainsi que les facteurs influençant son efficacité et intensité dans plusieurs régions du globe. Denman *et al.* (2007) ont souligné l'importance d'analyser les détails spatiaux et temporels afin d'isoler les mécanismes régionaux. Evans (1999) a indiqué que ces évaluations régionales étaient nécessaires pour déterminer les paramètres de modèles régionaux ou globaux d'estimation du flux vertical de carbone.

Quelques études et modèles ont marqué notre façon d'interpréter les flux verticaux de carbone. Eppley et Peterson (1979) ont décrit l'égalité entre la production nouvelle (basée sur la prise de l'azote allochtone par le phytoplancton) et la production exportée. Ils argumentent que dans un système

à l'équilibre, ces deux quantités sont forcément égales. Bien que Martin *et al.* (1987) ont permis de quantifier la décroissance du flux avec la profondeur, cette équation ne s'est pas avérée constante à travers les océans du globe et a été fortement revisitée par la suite (François *et al.*, 2002 ; Lutz *et al.*, 2002 ; Buesseler *et al.*, 2007b ; Honjo *et al.*, 2008 ; Buesseler et Boyd, 2009). Laws *et al.* (2000) ont développé un modèle d'estimation de la quantité de matière exportée à l'échelle planétaire. À partir du taux net de photosynthèse et de la température de l'eau, ce modèle prédit la proportion de production totale qui est exporté hors de la zone euphotique.

Plusieurs auteurs ont tenté de synthétiser les connaissances sur la pompe biologique à l'échelle globale. Turner et Ferrante (1979) ont consacré une première revue de littérature sur l'importance des pelotes fécales dans les processus de sédimentation de la matière organique. Turner a ensuite fait un état des connaissances globales sur la sédimentation de la matière organique en 2002 puis en 2015 (Turner, 2012, 2015). Dans ces deux papiers, il a discuté des différents types de particules sédimentant et couvert dans le dernier le mécanisme de la pompe biologique en résumant les connaissances sur son efficacité et sa variabilité. Boyd et Trull (2007) ont analysé et résumé les résultats d'études principalement issues du programme JGOFS. Ils font ainsi un point sur l'état des connaissances depuis 1999 et mettent l'accent sur l'importance de tenir compte de la complexité régionale dans l'élaboration de modèles globaux. Motivés par la non-applicabilité de l'équation de Martin *et al.* (1987) à de nombreuses observations, plusieurs auteurs se sont intéressés à l'efficacité de la pompe biologique. L'efficacité se définit comme le pourcentage de matière organique produite dans la zone euphotique exporté à la base de la zone mésopélagique (environ 2 km de profondeur). François *et al.* (2002) ont ainsi combiné les résultats de 68 pièges à particules profonds répartis dans les océans du monde. Ils ont notamment montré le rôle des carbonates en tant que lest pour la matière organique. Lutz *et al.* (2002) ont

quant à eux combiné les résultats de 180 pièges à particules et ont ainsi estimé l'efficacité de la pompe dans tous les océans de la planète. De la Rocha et Passow (2007) se sont intéressés aux processus biologiques et physiques impliqués dans l'efficacité de la pompe, ainsi qu'à leurs interactions. Ils soulignent le rôle des particules exopolymériques transparentes (en anglais, « transparent exopolymeric particles ») (TEPs) dans le processus d'agrégation ainsi que les rôles de la silice biogénique (frustules de diatomées) et du carbonate de calcium comme lests accentuant la vitesse de chute de la matière organique. Honjo *et al.* (2008) ont synthétisé les résultats de 134 pièges à particules en eau profonde et ont ainsi pu estimer les flux de COP, de carbonate de calcium, et de silice biogénique à la base de la zone mésopélagique. Ils définissent ainsi des zones océaniques dominées par l'influence de la silice biogénique (20% de la surface océanique mondiale, principalement dans l'océan Pacifique Nord et l'océan Austral) et d'autres où le carbonate de calcium est prépondérant (80% de la surface océanique mondiale). Buesseler et Boyd (2009) ont résumé les résultats de plusieurs jeux de données dont ceux du programme VERTIGO. Cette synthèse leur a permis de proposer deux nouvelles variables pour caractériser l'efficacité de la pompe biologique. La première est le « ratio Ez », définie comme le flux de COP à la base de la zone euphotique (Ez) divisé par la production primaire nette (sur l'ensemble de la zone euphotique). La seconde est « T₁₀₀ », définie comme le flux de COP à la base de la zone euphotique divisé par le flux de COP, 100 m sous la base de la zone euphotique. Ces nouvelles variables permettent de mieux caractériser les différents régimes océaniques en termes de flux d'export depuis la surface et d'atténuation du flux sous la zone euphotique. Zetsche et Ploug (2015) ont quant à eux réalisé un inventaire des molécules suspectées de jouer un rôle dans les processus d'agrégation de la matière organique. Riebesell *et al.* (2009) se sont intéressés à l'impact des changements climatiques sur le cycle du carbone. Ils ont réalisé une ébauche de leurs effets potentiels sur la pompe biologique et évalué l'ordre de grandeur de ces effets.

1.3. Les méthodes de mesures des flux verticaux

Deux grandes méthodes ont été régulièrement utilisées pour mesurer les flux verticaux de matière particulaire *in situ* : les pièges à particules et le déséquilibre ^{234}Th : ^{238}U (François *et al.*, 2002 ; Lutz *et al.*, 2002 ; Waples *et al.*, 2006 ; Honjo *et al.*, 2008). Le concept de piège à particules est simple : on place dans la colonne d'eau, à une profondeur connue, un réceptacle avec une ouverture d'une surface donnée pendant un temps donné. Souvent, plusieurs échantillons sont collectés sur la durée de mouillage du piège afin d'augmenter la résolution temporelle. Le piège, durant son déploiement, capte la matière sédimentant dans la colonne d'eau. Lors de la récupération du piège, on peut donc analyser la quantité de matière capturée par le piège ainsi qu'identifier la nature des particules. Il existe deux grandes familles de pièges : les dérivants et les fixes. Les pièges à particules dérivants ont une flottabilité neutre à une profondeur choisie et sont déployés pour une période s'étendant généralement de 12 à 24 h, durant laquelle ils dérivent au gré des courants. L'avantage de ceux-ci est qu'ils génèrent peu de biais hydrodynamiques et que le matériel est collecté rapidement, ne nécessitant donc pas nécessairement l'emploi d'un fixateur (Buesseler *et al.*, 2007a). Leur usage est recommandé dans les zones peu profondes, où les courants sont plus élevés. Cependant, bien qu'ils offrent une résolution temporelle élevée, leur déploiement et récupération demande beaucoup de temps et il est donc compliqué de les utiliser à fréquence élevée. En conséquence, les études se basant uniquement sur des pièges dérivants interprètent des résultats saisis ponctuellement, manquant probablement une partie des événements qui peuvent caractériser un écosystème pélagique. Les pièges à particules fixes sont montés sur un mouillage (un câble ancré au fond de l'océan) à une profondeur donnée. Leur déploiement est généralement plus long et peut aller de quelques jours à plus d'une année. Bien qu'ils génèrent plus de biais hydrodynamiques que les pièges dérivants (Buesseler, 1998), ils assurent de ne pas manquer d'événement durant

la durée de leur déploiement. Leur temps d'immersion contraint à l'utilisation d'un fixateur, ce qui peut entraver certaines analyses en laboratoire. Un problème majeur de l'utilisation de ces pièges est le biais que peut provoquer le zooplancton nageur. Il s'agit de zooplancton effectuant des migrations verticales, pouvant s'introduire dans le piège pour consommer le contenu des échantillons. L'utilisation d'un fixateur et d'un « nid d'abeilles » (structure servant à la fois à limiter le biais hydrodynamique et à empêcher le zooplancton de grande taille d'entrer dans le piège) résout partiellement ce problème. La méthode d'estimation du flux vertical via le déséquilibre $^{234}\text{Th} : ^{238}\text{U}$ est basée sur un principe chimique. La quasi-totalité de l'uranium dans l'eau de mer, se trouve sous forme dissoute et sa répartition dans l'océan est conservative (Coale et Bruland, 1985). En revanche, la forme dissoute de l'isotope ^{234}Th (temps de demi-vie = 24,1 j), produit constamment par la dégradation de ^{238}U , a une forte affinité pour la matière particulaire, sur laquelle elle se fixe par adsorption. Des profils de concentration de ^{238}U et de ^{234}Th en forme dissoute et particulaire dans la colonne d'eau (desquels on peut calculer les ratios $^{234}\text{Th}_{\text{dissous}} : ^{238}\text{U}_{\text{dissous}}$ et $^{234}\text{Th}_{\text{dissous}} : ^{234}\text{Th}_{\text{particulaire}}$) permettent d'estimer le taux de formation de particules ainsi que leur taux d'export. Ces mesures sont particulièrement utiles dans la zone euphotique, où la formation de particules est plus importante. Cependant, l'exactitude de cette méthode dépend fortement des types de particules qui composent le flux de carbone (Moran *et al.*, 2003 ; Passow *et al.*, 2006 ; Lalande *et al.*, 2008). En effet, le ^{234}Th présente une affinité différente pour des particules de tailles et de compositions différentes (Passow *et al.*, 2006). Elle est également sensible à la méthode d'échantillonnage qui varie souvent d'une étude à l'autre (par exemple pièges à particules, rosettes ou pompes ; Passow *et al.*, 2006). Les flux d'export mesurés par la méthode du ^{234}Th sont fréquemment plus élevés que ceux mesurés par pièges à particules (Moran *et al.*, 2003). Haskell *et al.* (2013) avancent que les flux estimés via la méthode au ^{234}Th sont plus représentatifs du carbone disponible pour la communauté pélagique proche de la surface

tandis que les pièges à particule donnent un meilleur estimé du carbone exporté vers de plus grandes profondeurs.

Ainsi Moran *et al.* (2003) ont avancé que les estimations du flux d'export pouvaient varier d'un facteur 2 à 10. Cet écart peut être occasionné par des différences de méthodologie, de région ainsi que de taille et composition des particules composant le flux (Lalande *et al.*, 2008).

1.4. Les particularités de l'Atlantique Nord et des régions de haute latitude

En régions tempérées et de hautes latitudes, les flux verticaux varient temporellement au rythme des saisons (Romero *et al.*, 2000 ; Tian *et al.*, 2001 ; Hargrave *et al.*, 2002 ; Lalande *et al.*, 2016). Dans ces régions, la dynamique de l'écosystème pélagique est fortement liée à la croissance du phytoplancton. Celle-ci est caractérisée par des floraisons printanières et parfois automnales, qui surviennent lorsque les conditions de la colonne d'eau permettent un apport simultané de lumière et de nutriments (Tian *et al.*, 2000 ; Behrenfeld, 2010 ; Chiswell, 2011). Les floraisons sont responsables de la formation d'une quantité importante de matière organique particulaire (MOP), assimilable par le réseau trophique pélagique. En conséquence, les espèces qui dépendent directement ou indirectement du phytoplancton, ont un cycle de vie axé sur le cycle de ce dernier (Edwards et Richardson, 2004). Dans ces écosystèmes, on observe généralement des pics de flux verticaux de MOP proches des floraisons phytoplanctoniques car celles-ci occasionnent une forte production et transformation de MOP. Les flux sont généralement plus faibles le reste de l'année car la croissance phytoplanctonique est ralentie.

On estime que l'Atlantique Nord joue un grand rôle dans la séquestration du carbone anthropique comparativement à sa taille (Sabine *et al.*, 2004). Les estimations actuelles attribuent à la pompe biologique de l'océan Atlantique Nord un taux d'export de 0,55 à 1,94 Gt C an⁻¹ pour une moyenne de 1,27

Gt C an⁻¹ (Sanders *et al.*, 2014). Les mers marginales, généralement plus productives (Laws *et al.*, 2000), ont été sous-étudiées en comparaison et sont rarement comptabilisées dans les évaluations globales (Antia *et al.*, 2001 ; Sabine *et al.*, 2004). Des modèles d'évaluation globale plus précis devront donc forcément tenir compte d'études réalisées dans les régions côtières.

1.5. Le GSL et le motif d'une nouvelle étude

Le GSL, objet de la présente étude, est une mer semi-ouverte de 226 000 km² située sur la côte Est du Canada et communiquant avec l'océan Atlantique Nord. Sous l'influence de processus estuariens et océaniques, le GSL montre une forte hétérogénéité spatiale. Pour cette raison, différentes zones ont été l'objet d'un échantillonnage intensif durant le programme canadien du JGOFS (Fig. a). Des pièges à particules dérivants avaient alors été déployés à 50 m et 150 m au printemps, en été et en automne pour des périodes d'approximativement 24 h. Un mouillage, incluant un piège à particules fixe à 150 m, avait également été placé pour un période de 4 mois couvrant l'hiver. Les résultats obtenus ont permis d'estimer l'intensité et de caractériser la composition du flux vertical de MOP (Rivkin *et al.*, 1996 ; Romero *et al.*, 2000 ; Roy *et al.*, 2000a ; Savenkoff *et al.*, 2000 ; Romero-Ibarra et Silverberg, 2011). Des variables ont été mesurées dans la colonne d'eau parallèlement aux flux verticaux, ce qui a permis la production de modèles tenant compte des flux de matière ainsi que des réservoirs (Tian *et al.*, 2000 ; Vézina *et al.*, 2000). Plus tard, Le Fouest *et al.* (2005) ont développé un modèle permettant d'estimer les moyennes annuelles de la production primaire, de la production secondaire et de la production de pelotes fécales dans les 45 premiers mètres de la colonne d'eau sur l'ensemble du GSL. Les résultats ont mis en évidence la grande hétérogénéité spatiale de cette production dans le GSL.

La présente étude a plusieurs raisons d'être. Elle s'inscrit dans la volonté de mieux quantifier régionalement les flux verticaux de carbone. Le dernier

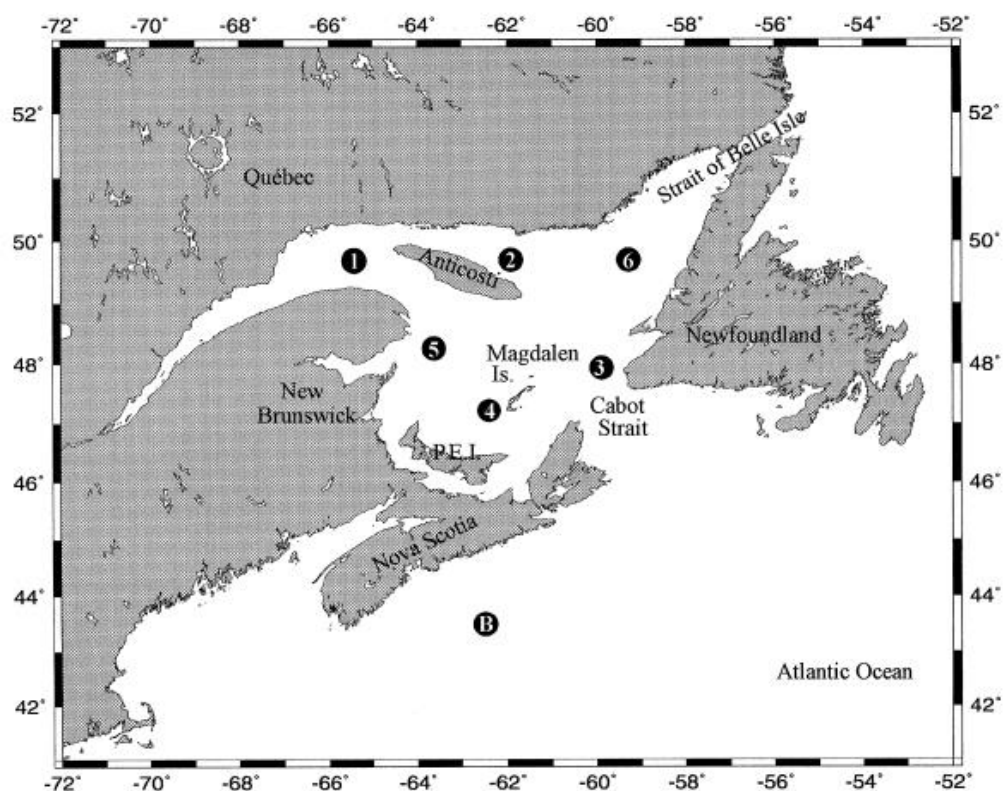


Figure a. Localisation des pièges à particules dérivants (stations 1 à 6) et fixes (stations 1 et B) déployés de 1992 à 1995 durant le programme Canadien du JGOFS dans le golfe du Saint Laurent et l’océan Atlantique. Adapté de Roy *et al.* (2000b)

échantillonnage de ces flux dans le GSL a eu lieu de 1992 à 1995, lorsque le niveau de CO₂ atmosphérique était d’environ 40 ppm plus bas (Le Quéré *et al.*, 2016). Or, on sait que la température de l’eau du GSL (surface intermédiaire et profonde) a augmenté et que le volume de glace a diminué pendant cette période (Galbraith *et al.*, 2016). En revanche, aucune tendance n’a été observée pour l’instant au sujet des concentrations en nutriments ou de la biomasse chlorophyllienne. Leurs importantes variations interannuelles seraient dues au brassage de la colonne d’eau de surface pendant l’hiver (Plourde et Therriault, 2004). Dans un contexte de changement rapide des conditions climatiques, il nous semble important d’intensifier les évaluations des flux verticaux de carbone dans le GSL. Ceci permet de mesurer les réponses du système aux

changements en cours et permet aussi à des modélisateurs d'utiliser les données à jour afin d'effectuer des prédictions. Nous savons à l'heure actuelle que le modèle de Le Fouest *et al.* (2005) produit des valeurs aberrantes de la production primaire totale et nouvelle dans les zones à caractère océanique du GSL (Le Fouest *et al.*, 2006, 2010 ; Laliberté *et al.*, 2018). La surestimation de la production phytoplanctonique dans ce secteur du Golfe est reliée, entre autres, à une mauvaise paramétrisation des conditions lumineuses de la colonne d'eau (Le Fouest *et al.*, 2010). Enfin, cette étude représente une opportunité de s'intéresser à la nature des particules sédimentant dans la colonne d'eau et d'ainsi avoir un aperçu sur les processus d'écologie planctonique ayant cours dans le GSL.

Les objectifs de la présente étude sont les suivants :

- (1) Mesurer et caractériser le flux vertical de matière organique particulaire ;
- (2) Comparer les résultats avec ceux obtenus durant le programme canadien JGOFS ;
- (3) Discuter les aspects écologiques des contributions saisonnières des particules chutant dans la colonne d'eau.

Pour atteindre ces objectifs, nous avons mouillé deux pièges à particules durant une année complète dans le GSL, à la marge du chenal Laurentien dans une région caractérisée par l'influence d'eaux provenant de l'Atlantique (El-Sabh, 1976 ; Savenkoff *et al.*, 2000).

**2. ANNUAL CYCLE OF THE PARTICULATE
DOWNWARD FLUX IN THE GULF OF
ST. LAWRENCE: THE ROLE OF PLANKTONIC
ORGANISMS**

2.1. INTRODUCTION

The Gulf of St. Lawrence (GSL) is a semi-enclosed marginal sea located on the east coast of Canada and covering 226,000 km². The climate is subarctic so that this sea is characterized by seasonal ice cover and a multiple layer water column structure (Galbraith *et al.*, 2016). Two layers are observed in winter and spring (surface and bottom) and 3 layers are observed in summer and autumn. Due to the warming of surface waters and imprisonment of a cold intermediate layer, a remnant of the previous winter is situated between the surface and the bottom layers (generally between 50 and 100 m). An important trough, the Laurentian Channel, crosses the GSL with depths ranging from 300 m (near the Saguenay Fjord) to 600 m (at Cabot Strait), covering about half of the surface of the gulf. The GSL displays a wide range of oceanographic conditions, due to the combination of its estuarine and oceanic characteristics (Galbraith *et al.*, 2016; Devine *et al.*, 2017). A spring phytoplankton bloom usually takes place in spring after the retreat of sea ice and in some areas, a second smaller bloom in late summer or autumn (Tian *et al.*, 2000; Le Fouest *et al.*, 2005; Le Fouest *et al.*, 2006; Le Fouest *et al.*, 2010).

The sampling station was located north of Cabot Strait, close to the “Old Harry” oil prospect (see Archambault *et al.*, 2017), on the north-eastern margin of the Laurentian Channel (see map in the next section). The region is known to be oligotrophic and to have a North Atlantic character (Savenkoff *et al.*, 2000). This is due to its position within a seasonal gyre, influenced by waters of both Atlantic and estuarine origins (see El-Sabh, 1976; Galbraith *et al.*, 2015, 2016; Bourgault *et al.*, 2017). At Cabot Strait, the integrated nitrate concentrations in the upper 50 m are low, ranging from 200 to 400 mmol m⁻² at the end of winter (Devine *et al.* 2017). The euphotic zone depth varies seasonally from 24 m in fall to over 40 m in summer (Babin *et al.*, 1993; Savenkoff *et al.*, 2000).

Extensive sampling of fluxes has occurred in the GSL during the Canadian Joint Global Ocean Flux Study program (JGOFS). Fluxes were measured at several stations and

seasons from 1992 to 1995 using drifting sediment traps at 50 m and 150 m depth and a time-series sediment trap at 150 m (Rivkin *et al.*, 1996; Romero *et al.*, 2000; Roy *et al.*, 2000a, 2000b; Savenkoff *et al.*, 2000; Tian *et al.*, 2000; Vézina *et al.*, 2000; Romero-Ibarra and Silverberg, 2011). Results obtained varied as much as from 16 to 300 mg C m⁻² d⁻¹. Based on these results, Tian *et al.* (2000) argued that downward carbon transport to deep waters in the GSL takes place essentially via particle sinking. They estimated model-derived fluxes of about 20 g C m⁻² y⁻¹ at 50 m and 17 g C m⁻² y⁻¹ at 100 m in the Anticosti Gyre.

Based on the fluxes measured at four stations in April and June 1994, Rivkin *et al.* (1996) reported that biogenic carbon export was independent of new production and food-web structure in the GSL. They measured little variation in the amount of sinking POC, during (April) and after (June) the phytoplankton bloom. However, the composition of the flux varied: chlorophyll *a* (Chl *a*) fluxes were more important during the bloom period and fecal pellet fluxes were greater during the post-bloom period.

The GSL has undergone several changes in recent years. Rises in water temperatures (surface, intermediate and bottom) have been observed since 1985 and reductions in sea ice extent and ice season duration have been observed since 1980 (Bismuth *et al.*, 2015). Nitrate plus nitrite concentration and Chl *a* biomass have shown important variations from year to year, but no significant trend has been observed since 1999 (Devine *et al.*, 2017). Plourde and Therriault (2004) showed that variations in spring nitrate concentrations were due to winter convection and possibly impacted primary production.

Although fluxes in the GSL have been well documented during the Canadian JGOFS, data were collected at multiple stations using drifting sediment traps. Considering the strong spatial and temporal gradients of oceanographic conditions along the GSL (Le Fouest *et al.*, 2005), there is a great interest to focus on a single station throughout a complete annual cycle. Furthermore, new data are needed to allow greater accuracy of

carbon flux models or to monitor conditions through time to follow temporal trends and perhaps measure effects of present or future climate changes. In this context, the objectives of the present study are:

- (1) To measure and characterize the sinking flux of particulate organic matter in the GSL for a whole year;
- (2) To compare our results with those obtained during the Canadian JGOFS program;
- (3) To discuss the ecological aspects of the seasonal contributions of the sinking particles.

2.2. MATERIAL AND METHODS

2.2.1. Water column

Water sampling was conducted close to the mooring location onboard the CCGS *Hudson* in October 2014 and October 2015, the CCGS *Teleost* in March and August 2015, and the RV *Coriolis II* in June 2015 (Fig. 1). At each station, water samples were collected in duplicate at 0-5 m with a rosette sampler equipped with 10 or 12 L Niskin-type bottles and a Sea-Bird 911 Plus conductivity, temperature, depth (CTD) probe for salinity and temperature measurements. Water subsamples for the determination of nutrient (nitrate plus nitrite, phosphate and dissolved silicon) and Chl *a* concentrations were transferred into dark acid-washed bottles.

Water samples for nutrient analysis were stored at -80°C until analysis using a Seal Analytical (formerly Bran+Luebbe) AutoAnalyzer 3 (adapted from Grasshoff *et al.*, 1999). Samples for Chl *a* analysis were filtered on Whatman GF/F filters onboard the ships and stored at -80°C in the dark until analysis by fluorometry (Turner Designs 10-AU fluorometer for *Coriolis II* samples and Turner Designs Trilogy for the other expeditions) following the acidification method described in Parsons *et al.* (1984).

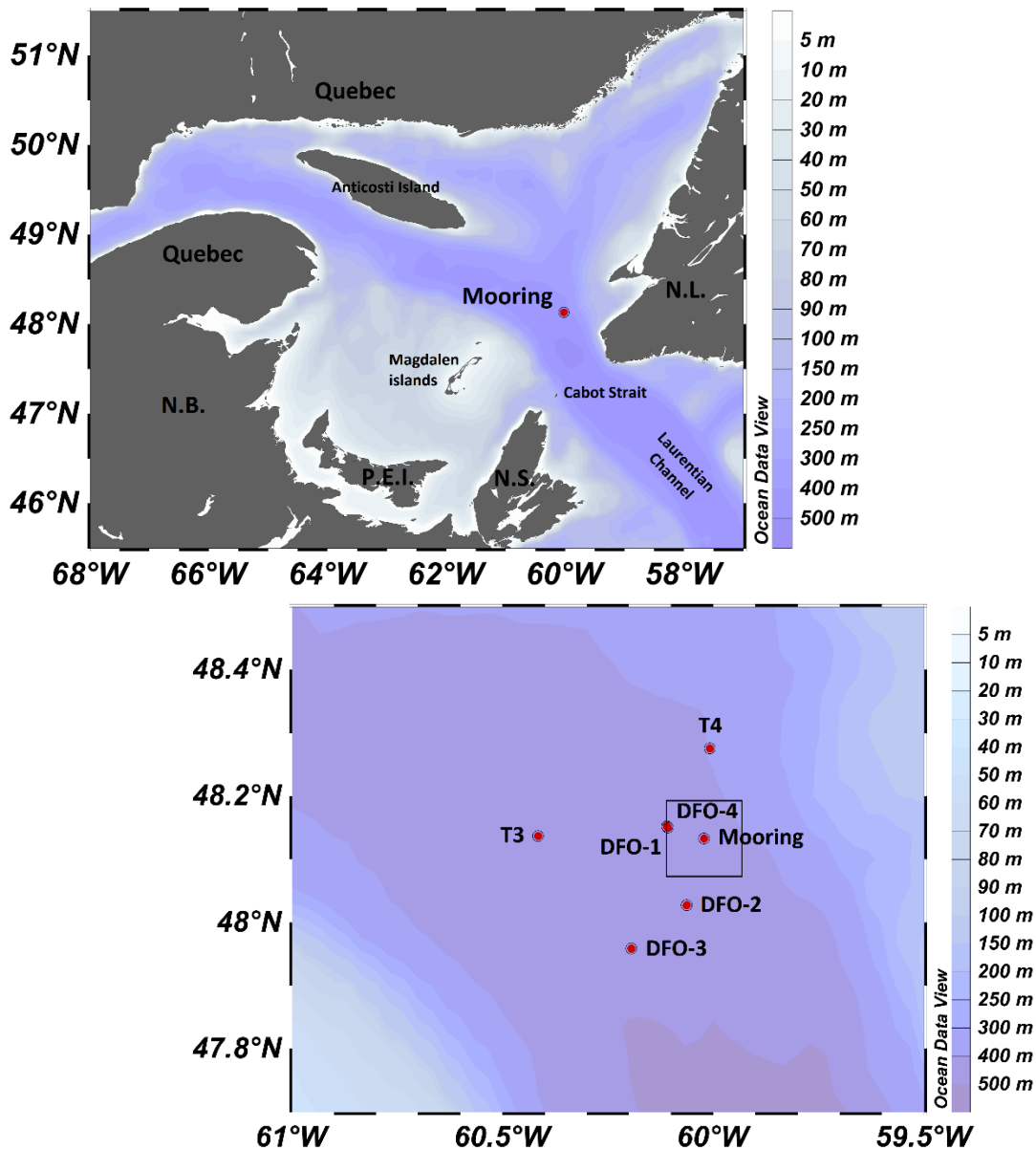


Figure 1. The Gulf of St. Lawrence with location of the mooring deployed from October 2014 to October 2015 and of the stations sampled by the CCGS *Hudson* in October 2014 and October 2015 and *Teleost* in March and August 2015 (DFO-1 to DFO-4) and by the RV *Coriolis II* in June 2015 (T3 and T4). The square indicates the area selected for averaged satellite-derived measurements

2.2.2. Satellite-derived measurements

Sea-surface temperature (SST) averages were obtained by Advanced Very High Resolution Radiometer (AVHRR) composites of 1.5-km resolution provided by the Bedford Institute of Oceanography (BIO) Operational Remote Sensing group (see Galbraith *et al.*, 2016). Sea ice cover data were obtained from the Canadian Ice Service as described in Galbraith and Larouche (2011). Surface Chl *a* data were obtained by level 3 MODIS satellite pictures of the study region (Bedford Institute of Oceanography Remote Sensing Laboratory). Sea ice cover and surface Chl *a* were estimated at the scale of 20×20 km centered on the mooring location (Fig. 1).

2.2.3. Sediment traps

2.2.3.1. Sample collection

Sinking material was collected at the northeastern margin of the Laurentian Channel ($48^{\circ} 07.980' N$, $60^{\circ} 01.30' W$; 461 m water depth; Fig. 1) using two Technicap PPS 6/2 sequential sediment traps fitted with a phenolic composite baffle (8 mm cell diameter) mounted in the opening. These traps have a conical shape (36°), an aspect ratio (height:diameter) of 6.25 and a collecting area of 0.5 m^2 . They were placed on a mooring line at 34 m and 100 m depth from 21 October 2014 to 1 November 2015. The original aim was to deploy the shallow trap at 50 m, i.e. below the base of the euphotic zone. However, a calculation error took place during the deployment. Both traps were equipped with a carousel comprising 24 sample cups of 255 ml each, filled with a 5% buffered formalin-seawater solution (Hargrave *et al.*, 2002) and rotating every 7 to 31 days (Table 1). After retrieval, samples were stored at 4°C in the dark until further analysis. The upper trap sample cups of October 2014, November 2014 and January 2015 were lost due to manipulation errors during the placement of the cups. Due to its position close to the surface, the upper trap baffle was colonized by various invertebrates (e.g. barnacles) during

summer. This may be due to the deepening of the euphotic zone in summer (Babin *et al.*, 1993; Savenkoff *et al.*, 2000). The results after 14 July 2015 were aberrant and thus rejected.

Table 1. Sampling period of each cup of the sediment traps moored at 34 and 100 m.

Sample cup	Opening	Closing
1	22 Oct. 2014	30 Oct. 2014
2	30 Oct. 2014	29 Nov. 2014
3	29 Nov. 2014	30 Dec. 2014
4	30 Dec. 2014	30 Jan. 2015
5	30 Jan. 2015	27 Feb. 2015
6	27 Feb. 2015	30 Mar. 2015
7	30 Mar. 2015	6 Apr. 2015
8	6 Apr. 2015	14 Apr. 2015
9	14 Apr. 2015	22 Apr. 2015
10	22 Apr. 2015	29 Apr. 2015
11	29 Apr. 2015	6 May 2015
12	6 May 2015	14 May 2015
13	14 May 2015	22 May 2015
14	22 May 2015	30 May 2015
15	30 May 2015	14 June 2015
16	14 June 2015	29 June 2015
17	29 June 2015	14 July 2015
18	14 July 2015	30 July 2015
19	30 July 2015	14 Aug. 2015
20	14 Aug. 2015	30 Aug 2015
21	30 Aug 2015	14 Sept. 2015
22	14 Sept. 2015	29 Sept. 2015
23	29 Sept. 2015	14 Oct. 2015
24	14 Oct. 2015	31 Oct. 2015

Trap samples were analyzed following the procedure described in Knap *et al.* (1996) following recommendations by Gardner (2000). In the laboratory, zooplankters

(“swimmers”) were removed from the samples using a 500 μm mesh and forceps. Samples were then split into subsamples for biological and chemical measurements.

2.2.3.2. Microscopy analyses

For each subsample, sinking material was diluted and sedimented to an appropriate concentration for counting (Lund *et al.*, 1958). Algal cells $> 4 \mu\text{m}$ and fecal pellets were counted, measured and identified using inverted microscopy (Wild Heerbrugg). To determine average cell sizes, up to 30 cells of each taxon were measured whereas all fecal pellets were measured.

Two different cell counts per subsample were performed: one at $450\times$ for phytoplankton and tiny protist identification and one at $135\times$ for larger protist identification. Biovolumes were estimated by attributing one or more basic geometrical shapes to cells (Hillebrand *et al.*, 1999; Olenina *et al.*, 2006) or by applying known length to volume equations (Thomsen, 1992). Cells were considered full if their protoplasm contained at least 60% of visible material. Identified cells $> 4 \mu\text{m}$ included autotrophic and heterotrophic protists, diatom and dinoflagellate spores, terrestrial plant pollens, and empty structures (diatom frustules, tintinnid loricae and silicoflagellate skeletons).

Biovolume to carbon conversion factors for the different taxa are shown in Table 2. All tintinnids observed in this study were all empty (i.e. without cellular content). A study by Karayanni *et al.* (2004) showed that 2% borated formalin did not significantly affect tintinnid loricae content. However, in this study, sample preservation in 5% borate buffered formalin and time of conservation prior to identification (2-2.5 years) might have. In addition, tintinnids being very fragile organisms (Sylvie Lessard, pers. comm.), sample manipulation might have affected the observations. Tintinnid loricae are thought to be made of proteinaceous material, containing carbon and nitrogen, and are known to sink in the water column even when empty. By doing so, they may play some role in vertical

fluxes (Agatha *et al.*, 2013). On the other hand, Buesseler *et al.* (2007a) recommended removing tintinnids from the samples and considering them as swimmers. Since empty tintinnid loricae probably contained little amounts of carbon compared to other biogenic particles, we assumed that these particles were not contributing to carbon fluxes in the present study.

One count was performed at $135\times$ for fecal pellets identification. Fecal pellets were classified following their condition (complete or in broken sections) and their shape (cylindrical or ovoid; Table 2). Biovolumes were estimated by attributing basic geometrical shapes to the fecal pellets (Hillebrand *et al.*, 1999). Biovolume to carbon conversion factors of fecal pellets are shown in Annex 1.

The total number of counted particles (including cells and fecal pellets) varied strongly from one sample to another. Hundred forty-six to 1363 cells were counted in samples 1 to 20, but only 99 to 127 were counted in samples 21 to 24 due to the scarcity of sinking matter that time of the year and a greater proportion of debris.

2.2.3.3. Chemical analyses

Duplicates for chemical analyses were sieved onto a $250\ \mu\text{m}$ silk mesh to remove the remaining large zooplankton. Subsamples for POC determination were filtered onto pre-combusted (450°C for 5 h) Whatman GF/F filters (nominal porosity of $0.7\ \mu\text{m}$). Inorganic carbon was removed by placing the filters overnight in a desiccator saturated with HCl fumes. Concentrations of POC were determined with a COSTECH 4010 CHN analyzer following the method described in Sharp (1974). Subsamples for Chl *a* and pheopigments determination (the sum of both will hereafter be named “pigments”) were filtered onto Whatman GF/F filters and $20\ \mu\text{m}$ silk mesh. Concentrations of pigments were determined by fluorometry (Turner Designs 10-AU fluorometer) following the acidification method described in Parsons *et al.* (1984). Subsamples for biogenic silica (BSi) determination were

filtered onto 0.8 μm Nuclepore polycarbonate membranes and 20 μm silk mesh. Concentrations of biogenic silica were determined with the NaOH alkaline digestion method of Ragueneau and Tréguer (1994).

2.2.4. Calculation

Since 11 trap samples were missing at 34 m, no annual flux was calculated at 34 m. Instead, fluxes at 34 and 100 m depth are compared for their available periods. The annual sinking flux of POC, BSi and pigments between 31 October 2014 and 31 October 2015 was estimated by trapezoidal integration. The same method was applied for the 6.5 months period where samples were available at both depths.

2.3. RESULTS

2.3.1. Surface water conditions

Sea ice was present over the study region from mid-February until the end of April 2015, reaching maximal coverage in mid-March (Fig. 2a). In 2015, sea ice appeared and remained later in the season relative to the climatology 2002-2017. Note that 2015 was the only year of the climatology where sea ice remained until the end of April. Galbraith *et al.* (2016) showed that sea-ice retreat occurred later than usual around Cabot Strait that winter. SST from satellite imagery decreased from the end of October 2014 and reached its minimal value (-1.8°C) in March 2015 (Fig. 2b). SST then increased from April 2015 to reach its maximal value (18.8°C) at the end of August 2015, after which it decreased again. *In situ* water temperatures were similar to satellite-derived measurements over the studied period. In contrast to temperature, surface salinity showed its maximum value in March 2015 (31.8 psu) and minimum in August 2015 (30.5 psu; Fig. 2c). Nutrients showed the same seasonal pattern as surface salinity, except in June (Fig. 2d, e). Surface nutrient concentrations were maximal in March 2015 (nitrate + nitrite = $6 \mu\text{mol L}^{-1}$; dissolved

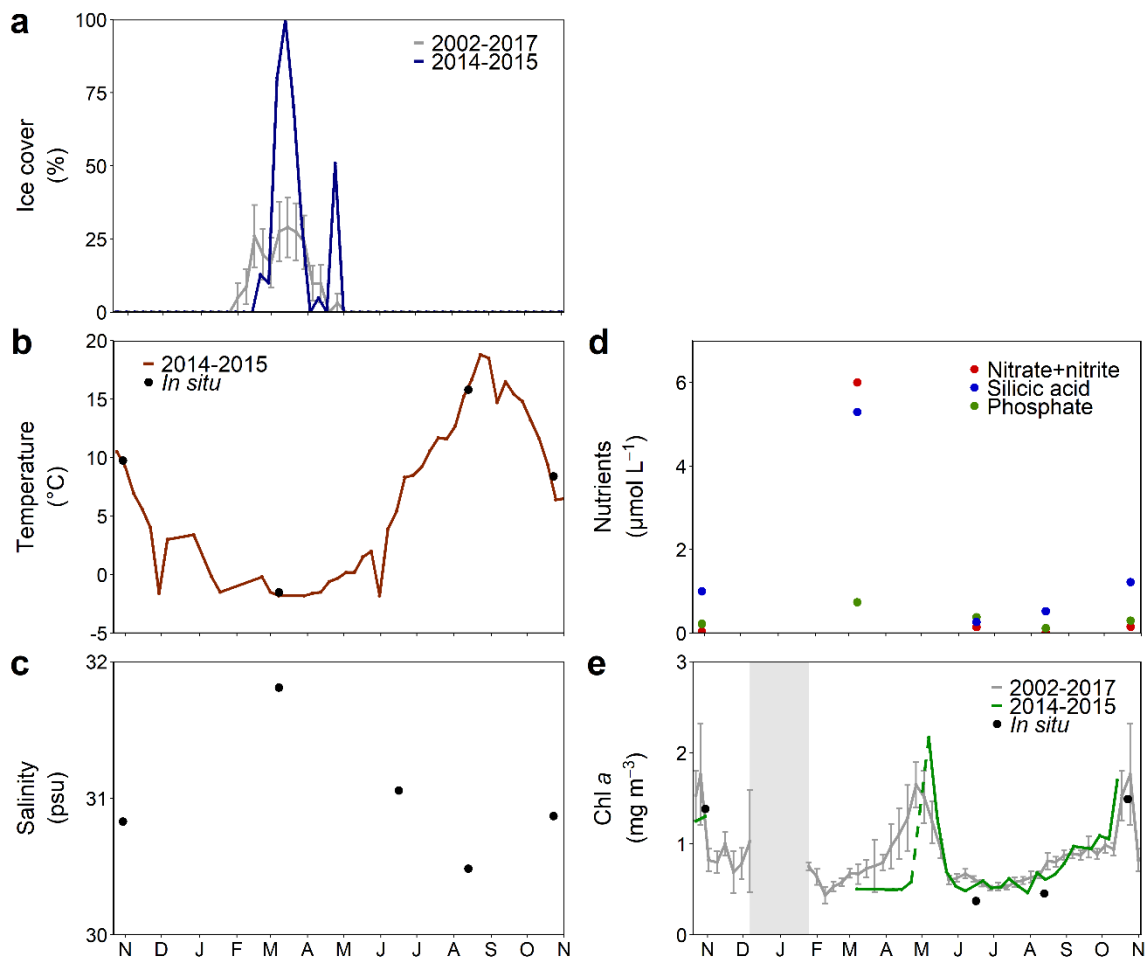


Figure 2. (a) Sea-ice concentration, and surface (b) temperature, (c) salinity, (d) nutrients and (e) chlorophyll *a* (Chl *a*) in the GSL from 2014 to 2015. Dots stand for “*in situ*” values, thus measured on discrete water samples whereas lines stand for satellite data. Climatologies for the period 2002-2017 are shown for Chl *a* and ice cover. In (a) and (e), bars are standard errors of the mean values. The dashed line in (e) indicates a missing value. The shaded area indicates missing data

silicon = $5.30 \mu\text{mol L}^{-1}$; phosphate = $0.74 \mu\text{mol L}^{-1}$; Fig. 2e). Dissolved silicon was minimal at the end of spring ($0.27 \mu\text{mol L}^{-1}$) and started rising during summer. Nitrate + nitrite and phosphate were minimal in mid-August 2015 ($0.02 \mu\text{mol L}^{-1}$ and $0.12 \mu\text{mol L}^{-1}$, respectively) and rose slightly in autumn. The molar ratios of nitrate + nitrite

to phosphate and of the nitrate + nitrite to silicic acid ranged from 0.18 to 8.11 and from 0.04 to 1.13, respectively. Based on satellite imagery data from 2002 to 2017, surface Chl *a* maxima usually occur at the April-May transition (Fig 2e). During the study period, the maximum value was observed on 7 May 2015 ($2.17 \mu\text{g L}^{-1}$). A second peak in surface Chl *a* ($1.70 \mu\text{g L}^{-1}$) happened in mid-October 2015 ($1.9 \mu\text{g L}^{-1}$), as also observed in the 2002-2017 climatology.

2.3.2. POC, BSi and pigment fluxes

Annual values for POC, BSi and pigments fluxes at 100 m were respectively $1.06 \text{ g C m}^{-2} \text{ y}^{-1}$, $1.52 \text{ g Si m}^{-2} \text{ y}^{-1}$ and $37.47 \text{ mg m}^{-2} \text{ y}^{-1}$. For the 6.5 months where data were available at 34 m, the fluxes of POC, BSi and pigments reached, respectively, values of 1.13 g C m^{-2} , 0.38 g Si m^{-2} and 7.62 mg m^{-2} at 34 m and 0.79 g C m^{-2} , 1.52 g Si m^{-2} and 37.35 mg m^{-2} at 100 m.

Fluxes of POC, BSi and pigments peaked in late April at both depths, except for POC at 34 m which peaked for two weeks until early May (Fig. 3). At 34 m, the values topped, respectively, at $36 \text{ mg C m}^{-2} \text{ d}^{-1}$, $32 \text{ mg Si m}^{-2} \text{ d}^{-1}$ and $571 \mu\text{g m}^{-2} \text{ d}^{-1}$ (Fig. 3a, c, e). At 100 m, they topped, respectively, at $29 \text{ mg C m}^{-2} \text{ d}^{-1}$, $132 \text{ mg Si m}^{-2} \text{ d}^{-1}$ and $3866 \mu\text{g m}^{-2} \text{ d}^{-1}$ (Fig. 3b, d, f). At 34 m, POC fluxes values dropped after the peak but remained elevated, and then continued to decrease until mid-July. At 100 m, values dropped markedly right after the peak and enhanced POC fluxes periods occurred in November, June and September. BSi fluxes were at least ten-fold lower year-round than during the peak. Pigment fluxes dropped markedly after the peak at both depths, however, the week right after the peak, fluxes remained elevated. Enhanced fluxes occurred in June at 34 m. At 100 m, fluxes remained elevated until mid-June.

Pigments were strongly dominated by pheopigments (from 62% to 95%; data not shown). The contribution of particles $< 20 \mu\text{m}$ to total pigment flux dominated during most

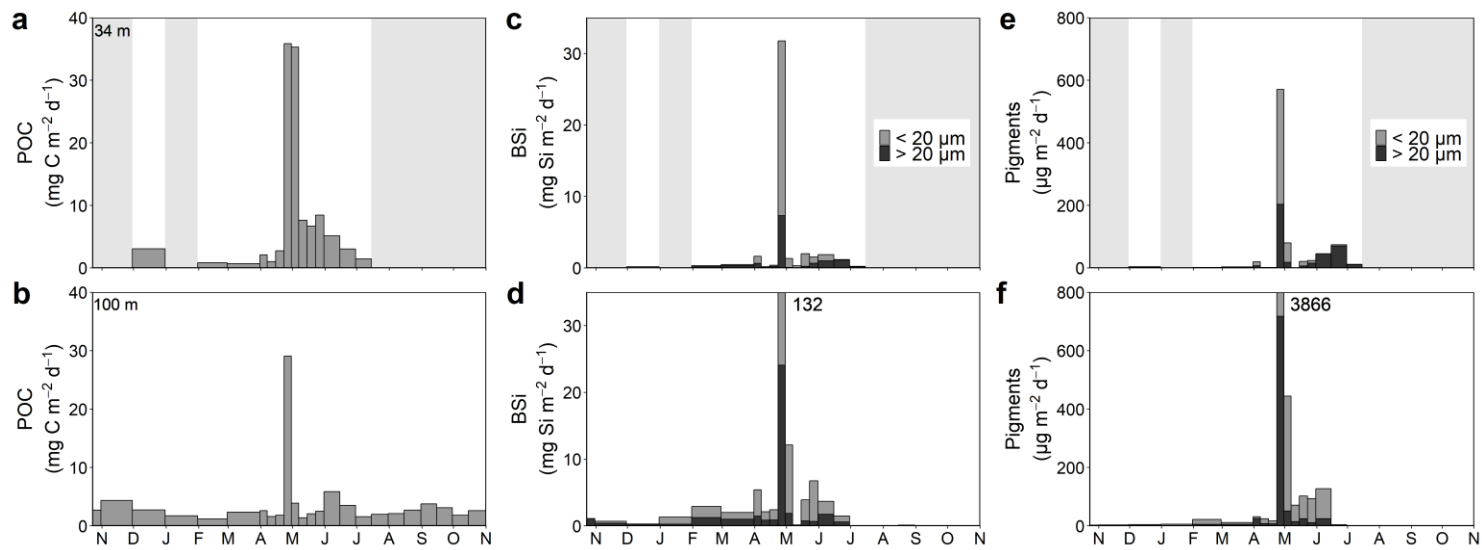


Figure 3. Mass fluxes of (a, b) POC, (c,d) BSi and (e, f) pigments (i.e. Chl *a* + pheopigments) with relative contribution of cells < 20 μm and cells > 20 μm at 34 m and 100 m depth from October 2014 to October 2015 in the GSL. Shaded areas indicate missing data

of the spring season at both depths and for both variables. Particles $> 20 \mu\text{m}$ made up a greater part of the pigment flux during summer, autumn and winter although their contribution rarely exceeded 50% for BSi. POC:pigments ratios varied consistently at 34 m, being lowest during the peaks of POC and pigment fluxes and the second half of June (see Annex 2). At 100 m, lowest values occurred in February and from the peaks of POC and pigment fluxes until mid-June.

2.3.3. Protist fluxes

2.3.3.1. Protist numerical fluxes

Numerical fluxes of protists peaked during the last week of April, with values of $14.0 \times 10^6 \text{ cells m}^{-2} \text{ d}^{-1}$ at 34 m and of $51.0 \times 10^6 \text{ cells m}^{-2} \text{ d}^{-1}$ at 100 m (Fig. 4a, b). Another enhanced period was observed in June at both depths. During these periods, diatoms totally dominated the numerical fluxes of protists and more exactly, pennate diatoms, except in June at 100 m (Fig. 4c-f). Protist carbon fluxes were higher at 100 m during the peak and at 34 m in June. They showed similar intensities at both depths the rest of the year with some variations.

Relative abundances showed an overall dominance of diatoms at both depths, especially during the peak of protist abundance (Fig. 4c, d). Coccolithophorids were present in December and in February at 34 m. At 100 m, they were present from late October 2014 to end of January and the second halves of September and October 2015. Dinoflagellates were present almost during the complete deployment at both depths, sometimes in very small numbers. At 34 m their relative abundance topped the second week of April. At 100 m, their major contribution occurred during summer and autumn.

Pennate diatoms were dominant for all the sampled periods at 34 m (Fig. 5e). At 100 m, pennate diatoms were dominant from November to late June, after what centric diatom took over (Fig. 5f). *Fragilariopsis* spp. appeared approximately around the protist

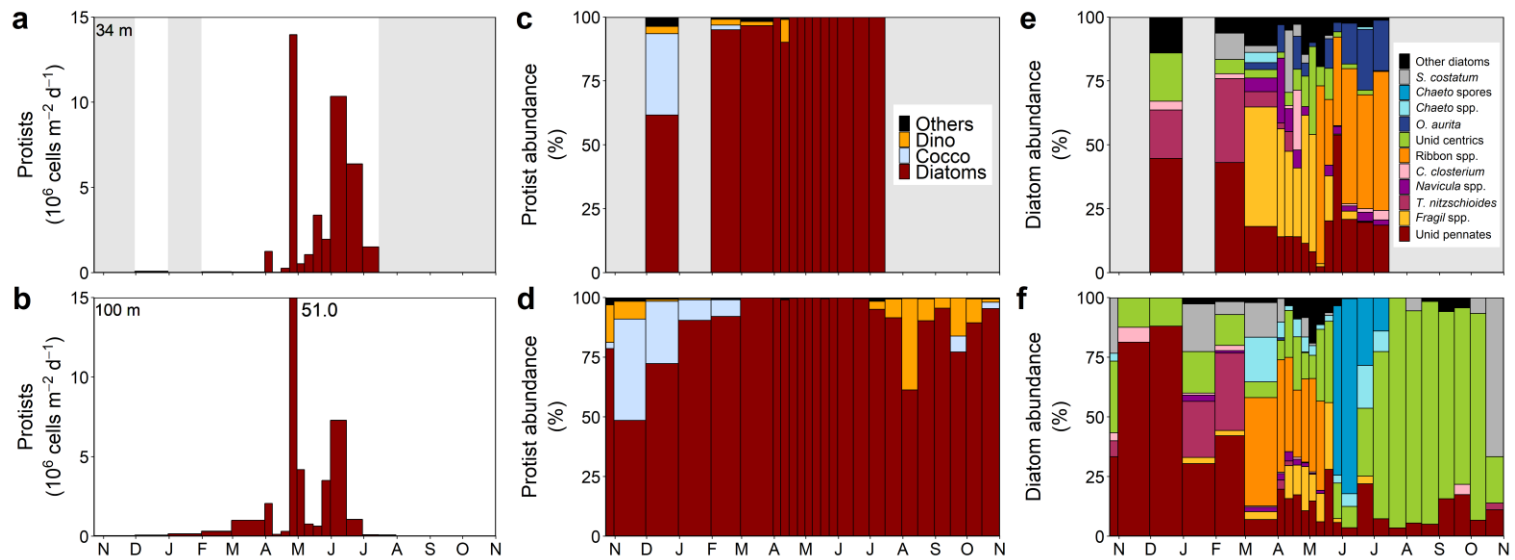


Figure 4. (a, b) Numerical fluxes of dominant protist taxa, (c, d) relative contribution of dominant protist taxa to total protist numbers in the sinking material (Dino: dinoflagellates, Cocco: coccolithophorids, Others: sum of all protist taxa contributing < 10 % of abundance at any time of the year) and (e, f) relative contribution of dominant diatom taxa to total diatom numbers in the sinking material (*S. costatum*: *Skeletonema costatum*, *Chaeto* spores: *Chaetoceros* spores, *Chaeto* spp.: *Chaetoceros* spp., *O. aurita*: *Odontella aurita*, Unid centrics: unidentified centric diatoms, Ribbon spp.: pennate ribbon spp., *C. closterium*: *Cylindrotheca closterium*, *T. nitzschioides*: *Thalassionema nitzschioides*, *Fragil* spp.: *Fragilariopsis* spp., Unid pennates: unidentified pennate diatoms, Other diatoms: sum of all diatom taxa contributing < 20 % of abundance at any time of the year) at 34 m and 100 m from October 2014 to October 2015 in the GSL. Shaded areas indicate missing data

abundance peak at both depths. Even if the taxa of pennate ribbon spp. were not identified, these diatoms were often observed at the same time as single cells of *Fragilariopsis* spp. and were about the same size. Thus, pennate ribbon spp. were thought to be mainly composed of *Fragilariopsis* spp. Pennate ribbons appeared from late spring to summer at 34 m but from late winter to mid-spring at 100 m. *Thalassionema nitzschioides* was present during a part of winter at both depths. *Skeletonema costatum* abundance was important during winter and early spring at both depths and at the end of October 2015 at 100 m. *Navicula* spp. and *Cylindrotheca closterium* relative abundances were significant in early spring at 34 m. *Odontella aurita* was present during spring-summer at 34 m. *Chaetoceros* spp. were present during the same period at 100 m. *Chaetoceros* spores were only observed at 100 m and were important from late May to mid-July. Unidentified pennate diatoms accounted for a large part of diatom numbers in December, February and late May at 34 m and in late autumn and winter at 100 m. Unidentified centric diatoms dominated diatom numbers from July to mid-October.

2.3.3.2. Protist carbon fluxes

Protist carbon fluxes peaked in late April and reached maximum values of $5.6 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 34 m and $11.2 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 100 m (Fig. 5a, b). During that period, diatoms dominated protist carbon in the sinking material (34 m: 65%; 100 m: 73%) and more exactly, centric diatoms (Fig. 5c, d). Enhanced fluxes periods also occurred the first week of April and during the month of June at 34 m, both dominated by diatoms as well. At 100 m, elevated fluxes occurred from mid-June to mid-August, first dominated by foraminifera and then by dinoflagellates. Protist carbon fluxes were higher at 100 m during the peak and of similar intensities at both depths the rest of the year with some variations.

Diatoms dominated the fluxes from February to mid-July at 34 m, except for two weeks (Fig. 5c). At 100 m, they dominated during most of winter and their contribution decreased at the beginning of spring, except for two weeks (Fig. 5d). Planktonic

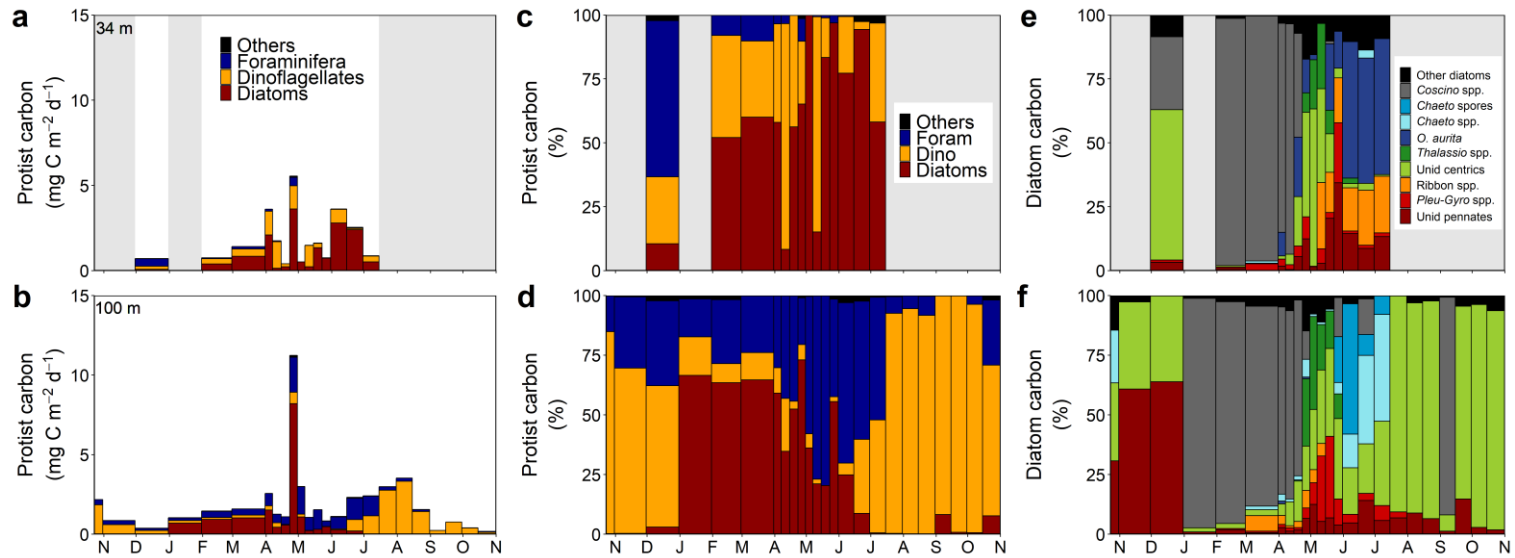


Figure 5. (a, b) Carbon mass fluxes of dominant protist taxa, (c, d) relative carbon contribution of dominant protist taxa to total protist carbon in the sinking material (others : sum of all types of protists contributing < 10 % of carbon at any time of the year, mainly small unidentified protists) and (e, f) relative carbon contribution of dominant diatom taxa to total diatom carbon in the sinking material (*Coscinoceros* spp.: *Coscinodiscus* spp., *Chaetoceros* spores: *Chaetoceros* spp., *Chaetoceros* spp.: *Chaetoceros* spp., *O. aurita*: *Odontella aurita*, *Thalassiosira* spp.: *Thalassiosira* spp., Unid centrics: unidentified centric diatoms, Ribbon spp.: pennate ribbon spp., *Pleurosigma* spp.: *Pleurosigma* and *Gyrosigma* spp., Unid pennates: unidentified pennate diatoms, Other diatoms: sum of all diatom taxa contributing < 20 % of carbon at any time of the year) at 34 m and 100 m from October 2014 to October 2015 in the GSL. Shaded areas indicate missing data

foraminifera were an important contributor at 100 m, being present most of the year and making a large deal of protist carbon in spring. At 34 m, they were important only in December. Dinoflagellates were present in both traps throughout the year and consisted by far mostly of heterotrophic *Protoberidinium* spp. (summer at 100 m; winter to spring at 34 m) with some autotrophic *Tripos* spp. (summer and winter) and some mixotrophic *Dinophysis norvegica* (mid-summer to autumn; data not shown). Their contribution was especially high during the second weeks of April and May at 34 m. At 100 m, dinoflagellates dominated the protist carbon fluxes from late-October 2014 to end-December and from mid-July to end-October 2015.

Centric diatoms were clearly dominant year-round at both depths, at the exception of late May at 34 m and of November to January at 100 m (Fig. 5e, f). Pennate diatom contribution rose during spring at both depths. *Coscinodiscus* spp. dominated during winter at both depths and remained a great contributor to the flux in early spring. They also dominated the flux the first half of September at 100 m. *Thalassiosira* spp. contributed significantly to the diatom carbon fluxes at both depths, from the protist carbon peak until late May. Pennate ribbon spp. participated to the flux from mid-spring to mid-July at 34 m but from late winter to mid-spring at 100 m. *Pleurosigma* and *Gyrosigma* spp. contributed mostly from late winter to late May at 34 m and mostly from the protist carbon peak to late July at 100 m. *O. aurita* was important during the spring-summer transition at 34 m and *Chaetoceros* spp. during the same period at 100 m. *Chaetoceros* spores were only observed at 100 m and were important from late May to mid-July. The great contributions of *Odontella aurita* in spring-summer at 34 m and of *Chaetoceros* spp. and *Chaetoceros* spores at 100 m during approximately the same period marked a great difference between both depths. Unidentified centric diatoms represented a great deal of the diatom flux in December and spring at 34 m and in autumn, spring and summer at 100 m. Unidentified pennate diatoms remained present throughout the year at both depths but dominated only from November to January at 100 m.

2.3.4. Fecal pellet carbon fluxes

Fecal pellet carbon (FPC) fluxes peaked in early May at 34 m and reached a maximum value of $2.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 6a). At 100 m, they peaked in late April with a value of $19.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 6b). Broken pellets dominated during the peak of FPC at 34 m (72%), followed by cylindrical pellets (26%; Fig. 6c). At 100 m, the peak was dominated by cylindrical pellets (65%) and the fluxes remained elevated for 3 more weeks after the peak, still dominated by cylindrical pellets (Fig. 6d). Also, FPC fluxes were generally higher at 100 m, where fecal pellets were observed year-round. Cylindrical pellets were present nearly year-round, with elevated contributions to fecal pellet carbon fluxes in winter, a part of spring and early July at 34 m, and in spring and a part of winter at 100 m. Ovoid pellets were important most of spring at 34 m and in winter, autumn and most of summer at 100 m. Broken pellets, composed of both types of shapes were present year-round at both depths with largest contributions in spring, early summer and during the second half of September. FPC fluxes were generally higher at 100 m except for the second week of April.

2.3.1. Biogenic organic carbon fluxes

Combined, protist plus fecal pellet carbon fluxes, hereafter named biogenic organic carbon (BC) fluxes, contributed, on average, 85.5% (range: 8-206%) and 72.9% (range: 7-168%) of the total POC sinking flux at 34 m and 100 m, respectively (see Annex 2). They peaked in late April at both depths with a value of $6.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 34 m and of $30.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 100 m (Fig. 6a, b). In addition, the compositions of the sinking material during the peak at both depths were different, being dominated by fecal pellets (63%) at 100 m and by diatoms (59%) at 34 m (Fig. 6c, d). A week later, the flux at 34 m was dominated by fecal pellets (82%). Fecal pellets made a large contribution to the BC fluxes the third week of April and first of May at 34 m and from mid-April until mid-June at 100 m. Protists were from far the major contributors the rest of the year. Although BC

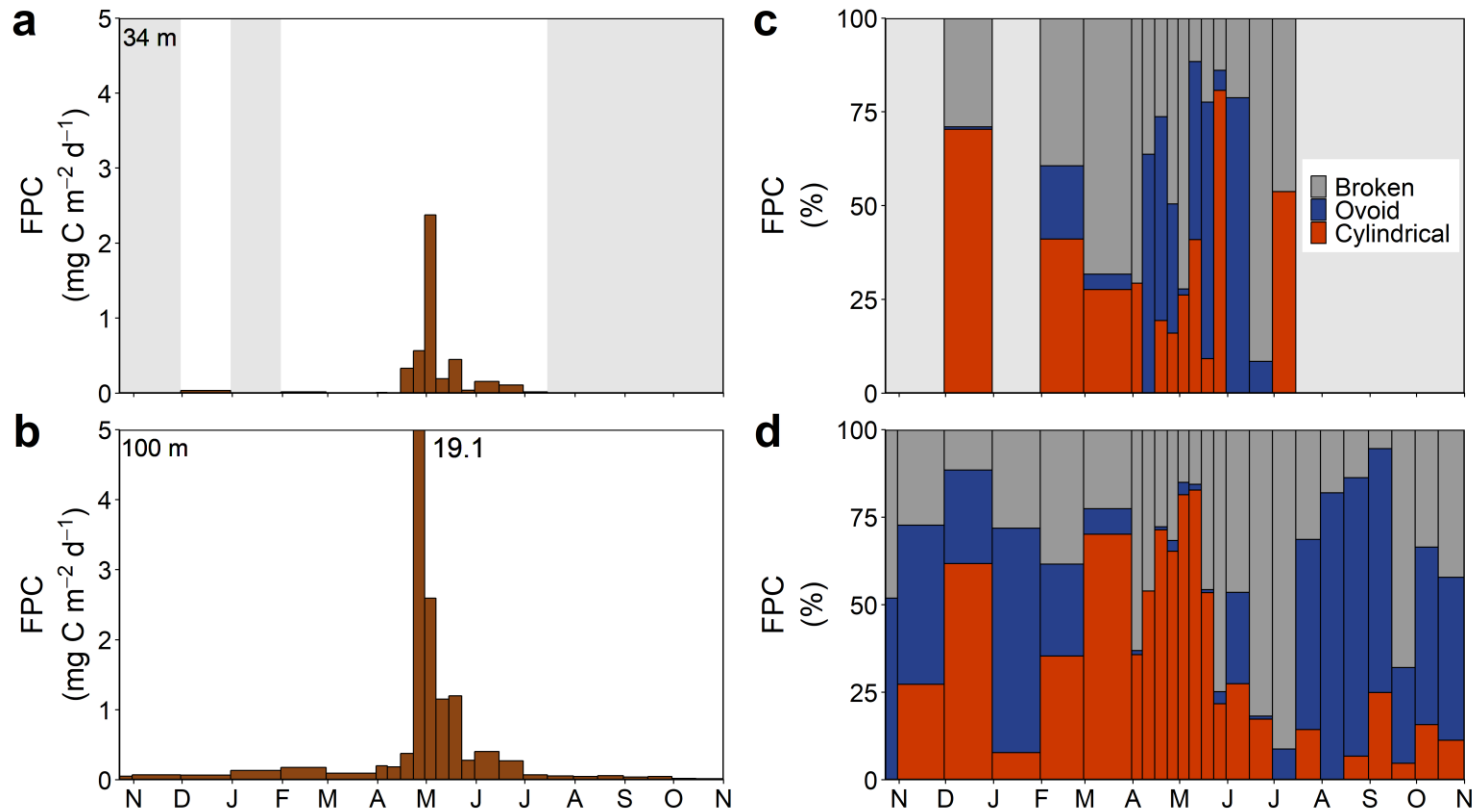


Figure 6. (a,b) Carbon mass fluxes of zooplankton fecal pellets and (c,d) relative carbon contribution of fecal pellet types to total fecal pellet carbon in the sinking material at 34 m and 100 m from October 2014 to October 2015 in the GSL. Shaded areas indicate missing data

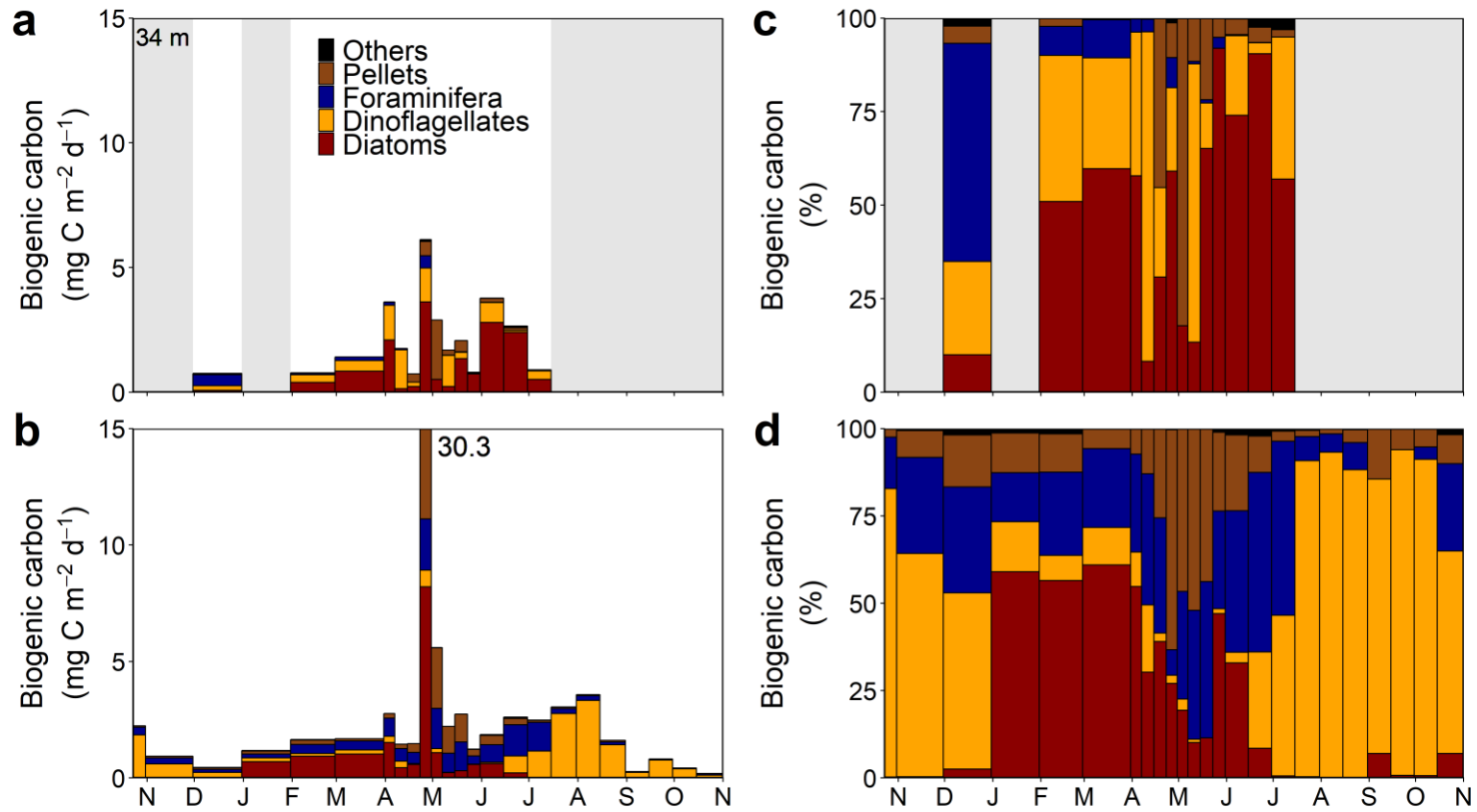


Figure 7. (a,b) Carbon mass fluxes of dominant identified particles (Others: sum of all types of particles contributing < 10 % of carbon at any time of the year, mainly pollens and small unidentified protists), (c,d) relative carbon contribution of identified particles to total identified particles carbon at 34 m and 100 m from October 2014 to October 2015 in the GSL. Shaded areas indicate missing data

fluxes peaked higher at 100 m, they were generally of similar intensities at both depths with some variations.

2.4. DISCUSSION

2.4.1. Export flux timing and magnitude in the GSL

POC, BSi and pigment fluxes peaked shortly after the retreat of sea ice and a couple of days before the peak of surface Chl *a* (Figs. 2a, e and 3). Surface water temperatures and air temperatures were lower than normal during winter 2014-2015 (Galbraith *et al.*, 2016). Hence, a large volume of sea ice was produced that year in the GSL and drifted over the mooring from mid-February until the end of April (Fig. 2a). The augmentation of ice cover in late April in the climatology is due to the value of 2015 only. Thus, the longer than average presence of sea-ice seems to have delayed the peak of Chl *a* that year. Due to cloud cover, there was no available surface Chl *a* satellite data over the study region around the April-May transition. The second peak in surface Chl *a* in mid-autumn (Fig. 2e) was not associated with greater fluxes in POC, BSi and pigments at 100 m. This may indicate that the particulate matter was intensely recycled by the food web in the upper water column during that time of the year. The importance of heterotrophic dinoflagellates during the same period supports this hypothesis (Fig. 5). It may also be that the small centric diatoms observed during that period did not sink in great numbers at 100 m. Our results are in good accordance with the model of Le Fouest *et al.* (2005), which predicts that the phytoplankton bloom in the Laurentian Channel usually happens at the end of April, after the retreat of sea ice.

The peaks of the POC, BSi and pigment fluxes contrasted strongly with the fluxes observed the rest of the year and represented respectively 34%, 74% and 80% of the annual fluxes at 100 m. This enlightens the importance of the bloom for the export of biogenic matter in the GSL. The molar ratios of nitrate + nitrite to phosphate and of the

nitrate + nitrite to silicic acid were generally lower than the critical N:P value 16 and N:Si of 1.1 (Redfield *et al.* 1963; Brzezinski, 1985). Thus, as dissolved nitrogen was the nutrient in lowest concentration relative to the phytoplankton nutrient requirement, phytoplankton (mainly diatoms; Fig. 5) related fluxes dropped drastically after its consumption. Moreover, they remained much lower during the rest of the productive season as measured surface concentrations of nitrate did not exceed $0.2 \mu\text{mol L}^{-1}$. The smaller percentage of POC export during the peak compared to the annual flux may be explained by the important contributions of other protists (containing no BSi and no or less pigments; e.g. heterotrophic dinoflagellates, planktonic foraminifera), fecal pellets and detritus to the fluxes the rest of the year.

Peak and annual POC fluxes values measured in this study were very low compared to previous studies in the GSL, in the Northwest Atlantic Ocean and in other subarctic and arctic seas (Table 2) but are consistent with recent studies showing that surface Chl *a* concentrations remain relatively low in the Cabot Strait region throughout the year (Devine *et al.*, 2017; Laliberté *et al.*, 2018). The maximum surface nitrate concentration was around $6 \mu\text{mol L}^{-1}$ during this study, a value similar to the mean integrated values measured in the upper 50 m of the water column since 2001 in March for the area (range: $2\text{--}8 \mu\text{mol L}^{-1}$, median: $6 \mu\text{mol L}^{-1}$; Devine *et al.*, 2017). The sampling area may thus be considered as oligotrophic as indicated by the low surface concentration of nitrate and Chl *a* and low sinking fluxes of particulate matter which persist after the spring bloom (Figs. 2d, e and 3). We think that the seasonal inflow of nutrient-poor Atlantic surface waters through Cabot Strait is the main factor of the low nutrient concentrations observed in the area (El-Sabh, 1976; Galbraith *et al.*, 2015, 2016).

2.4.2. Bloom and flux composition

Such as POC fluxes, BC fluxes peaked around the measured surface Chl *a* maximum and were about the same order of magnitude (Figs. 3 and 7). The high contribution of

diatoms and fecal pellets around the bloom is a common feature observed around the world (Turner 2002, 2015). The presence of various taxa of pennate and centric diatoms during the bloom is typical of this area of the GSL (Bérard-Therriault *et al.*, 1999). Especially, *Fragilariopsis* spp. are known to contribute in great numbers to bloom fluxes in the GSL (Romero *et al.*, 2000). Some species of *Fragilariopsis* spp. are known to occur soon in the season while there is still ice cover (von Quillfeldt, 2000). However, their relative contributions were much lower in terms of carbon due to their small biovolume (about 50-300 μm^3 in this study). Therefore, centric diatoms, including *Thalassiosira* spp., were the greatest carbon contributors among diatoms during that period. Romero-Ibarra and Silverberg (2011) made similar observations during the April 1994 bloom period, at four different stations in the GSL.

The high contribution of fecal pellets around the bloom period was due to the presence of metazooplankton grazers. Ovoid fecal pellets, important in FPC at 34 m during the peak of BC, could have been produced by various groups such as pteropods and small copepods (Kobari *et al.*, 2010; Manno *et al.*, 2010, 2015). Cylindrical pellets, that made up the most important contribution to FPC during the same period at 100 m, measured about 80-500 μm length and 55-170 μm width. These measurements usually correspond to calanoid copepod pellets (González and Smetacek, 1994, Romero-Ibarra and Silverberg, 2011) or hyperiid pellets (Kraft *et al.*, 2013). Cylindrical pellets were the largest contributors to FPC fluxes at 50 and 150 m in the study of Romero-Ibarra and Silverberg (2011). That contribution was associated with the dominance of *Calanus finmarchicus* and *Calanus hyperboreus* in the zooplankton community at the same time (Roy *et al.*, 2000).

2.4.3. Seasonality of the flux composition

BC fluxes results indicate a great change in contributions of organisms, consistent with the general classical Plankton Ecology Group model of seasonal succession developed

Table 2. Particulate organic carbon (POC) sinking fluxes measured during different studies at several subarctic and arctic locations. Superscripts stand for the type of sediment traps used in the studies: drifting (d) and mooring (m)

Depth (m)	Annual (g C m ⁻² y ⁻¹)	Peak value (mg C m ⁻² d ⁻¹)	Location	Study
100 ^m	1.1	29.1	Gulf of St. Lawrence (Laurentian Channel)	This study
50 ^d	/	~ 150	Gulf of St. Lawrence (multiple stations - 1994)	Rivkin <i>et al.</i> (1996)
50-150 ^d	15.3	118		
50 ^d	54.4	298		
150 ^m (autumn-winter)	14.2	60	Gulf of St. Lawrence (Anticosti Gye)	Romero <i>et al.</i> (2000); Romero-Ibarra and Silverberg (2011)
150 ^m (spring-summer)	1.9	16	Northwest Atlantic (Emerald Basin)	
196 ^m	2.0	~ 25	Eastern Fram Strait	Lalande <i>et al.</i> (2016)
260-340 ^m	1.58-2.45	~ 11-50	Eastern Fram Strait	Bauerfeind <i>et al.</i> (2009)
40 ^m	/	404	Conception Bay (Newfoundland)	Thompson <i>et al.</i> (2008)
80 ^m	/	516		
50 ^d	/	674	Northwest Atlantic Ocean	Pommier <i>et al.</i> (2008)
100 ^d	/	~ 400		

by Sommer *et al.* (1986), also named “PEG-model”. Diatoms, important consumers of dissolved silicon, were great contributors to the low BC fluxes in winter and early spring while concentrations of this nutrient were highest due to winter convection (Plourde et Therriault, 2004). At 100 m, their contribution decreased after the bloom, when the nutrient was presumably depleted in surface waters due to its consumption. At 34 m however, their contribution was important in late spring and early summer as well, when surface dissolved silicon concentration was low. *In situ* Chl *a* measured 16 km north of the mooring location on 16 June 2015 revealed the presence of a deep chlorophyll maximum (DCM) around 40 m depth. Thus, we believe that the high diatom contribution at 34 m, was mainly due to the proximity of the trap with the DCM. Levasseur *et al.* (1992) observed high diatom abundances in a DCM in the Northwest GSL at the end of July. However, diatoms probably represented a minor part of the surface phytoplankton biomass during summer, as suggested by the augmentation of surface dissolved silicon during that period but the diminution of nitrate. The export of *Chaetoceros* spp. and *Chaetoceros* spores during the spring-summer transition at 100 m is classical in the GSL that time of the year (Bérard-Therriault *et al.*, 1999). Spore formation in the genera *Chaetoceros* is known to be a resistance mechanism used to survive until the productive season (Oku and Kamatani, 1999). A lot of empty frustules of *Chaetoceros* spp. were found in this study at many times of the year, but little full cells were observed in comparison. It is possible that they were selected as a preferred prey for the zooplankton community (Schnack, 1985). The notable export of chain-forming *O. aurita* during the spring-summer transition at 34 m is consistent with the observations of Baars (1986) on the fast-growing ability of this species in cold temperatures. *O. aurita* is a known arctic and boreal diatom, usually present in the GSL from May to November (Cupp, 1943; Bérard-Therriault *et al.*, 1999). Although their abundance was very low, *Coscinodiscus* spp. totally dominated the low BC fluxes during the winter and early spring, with *C. centralis* composing most of the genus. Except for *C. radiatus* during the spring bloom in the St. Lawrence Estuary, *Coscinodiscus* spp. were not reported

to be an important species in this marine system (Bérard-Therriault *et al.*, 1999). The reported scarcity of this taxon in the water column versus its dominance in winter and early spring fluxes measured in this study may be explained by an inappropriate sampling of this large-sized phytoplankton (diameter up to 350 μm ; mean cellular volume of about $1.5\text{-}4.5 \times 10^6 \mu\text{m}^3$) by Niskin-type water bottles. Plankton net sampling may, however, give a more accurate estimation of their abundance and biomass in the upper water column (see Duerksen *et al.*, 2014). The very large sizes of species composing this taxon lead them to sink rapidly from the upper water column. Unidentified pennate and centric diatoms contributed to a large part of the diatom carbon fluxes throughout the year. They were mainly composed of small diatom cells (4-20 μm) difficult to identify properly by optic microscopy.

The dominance of dinoflagellates at 100 m suggests they took over diatoms after dissolved silicon depletion (Sommer *et al.*, 1986). The importance of *Protoperidinium* spp. during summer at 100 m and winter and spring at 34 m suggests that these dinoflagellates were located closer to the surface when their prey (i.e. diatoms) became important. *Protoperidinium bipes*, a widespread species of the genus, is known to feed on diatom blooms and to have an important grazing impact (Jeong *et al.*, 2004). In the same idea, a high biomass of *Protoperidinium* spp. had been reported during the 1992 spring bloom in the baie des Chaleurs (GSL; Tamigneaux *et al.*, 1987). *Protoperidinium* spp. are also known to be important in the GSL during summer (Bérard-Therriault *et al.*, 1999). Romero *et al.* (2000) observed great numerical contributions of dinoflagellates, including *Protoperidinium* spp., from May to November at several stations in the GSL.

Rising fecal pellet contribution before the bloom and enhanced contribution for several weeks after it reveal the match of the productive periods of both phytoplankton and zooplankton in the GSL. The dominant calanoid copepods, *C. finmarchicus* and *C. hyperboreus*, take advantage of the availability of their major prey, diatoms (Falk-Petersen

et al., 2009). The low POC:pigment ratios observed during that period at 100 m, suggest that fecal pellets contained phytoplankton. *C. finmarchicus* spends most of the unproductive season in diapause (Plourde and Runge, 1993; Plourde *et al.*, 2002; Maps *et al.*, 2010, 2011). A part of the population of *C. finmarchicus* may come out of dormancy as soon as in early or mid-winter and the whole population is usually active and starts to reproduce before the phytoplankton bloom (Plourde *et al.*, 2001; Maps *et al.*, 2011). A study in Disko Bay, western Greenland, showed that fecal pellet production rose even before the phytoplankton bloom for *C. finmarchicus* and during the bloom for *C. hyperboreus* (Swalethorp *et al.*, 2011). This may explain why cylindrical fecal pellets were important even before the Chl *a* maximum. The smaller role of ovoid pellets was also observed by Romero-Ibarra and Silverberg (2011). The high contribution of broken pellets in our study suggests that they may have been broken up during collection and sieving. However, *in situ* coprochaly and coprohexy may also have played a role on the loosening and fragmentation of pellets (Iversen and Poulsen, 2007).

The great contribution of foraminifera nearly year-round at 100 m reveal the importance of these organisms for the organic and inorganic (through sinking of their calcareous tests) exports of carbon in the GSL. Romero *et al.* (2000) observed great contributions of foraminifera to the numerical fluxes. To our knowledge, no study has focused on the distribution and ecology of planktonic foraminifera in the GSL. However, they are known to be abundant in the adjacent waters of the northwest Atlantic (Bé, 1959; Head and Pepin, 2010). As advection is known to affect the communities of foraminifera found in the sediments of the GSL (Bartlett and Molinsky, 1972), it is probable that the presence of foraminifera comes from the inflow of Atlantic waters through Cabot Strait (El-Sabh, 1976). Further investigations on these organisms in the GSL would be of great interest considering that they are probably an important component of the zooplankton community nearly year-round.

The presence of coccolithophorids, even in low abundance, had not yet been reported in the GSL for autumn and winter. Coccolithophorids (mostly *Emiliana huxleyi*) are known to form large blooms in the GSL and adjacent NW Atlantic waters (Brown and Yoder, 1994). They usually constitute a part of the phytoplankton community in summer (Bérard-Therriault *et al.*, 1999). Observations in the Gulf of Maine have shown that summer (June-July) blooms of *E. huxleyi* are usually related to oligotrophic conditions, with low micro- and macronutrient concentrations (Townsend *et al.*, 1994).

2.4.4. Differences in the magnitude and composition of the sinking fluxes between sampling depths

Great differences were observed between both sampling depths in terms of magnitude and composition of the fluxes. For the 6.5 months where samples were available at both depths, fluxes of POC were 1.4 times higher at 34 m; however, BSi and pigments fluxes were respectively 4.0 and 4.9 times higher at 100 m. Differences of composition were obvious from late winter to early summer: fecal pellet and foraminifera carbon contribution were far more important at 100 m, dinoflagellates were found mostly at 34 m in spring, Ribbon spp. dominated diatom abundance fluxes from late winter to mid-spring at 100 m but from mid-spring to early summer at 34 m and *O. aurita* and *Chaetoceros* spp. were important from late spring to early summer but not at the same depth (Figs. 4-7). Various mechanisms are thought to have contributed to these differences, such as the position of the upper trap in the photic zone, the lateral advection of the particles from adjacent waters, and the active transport of particles by zooplankton grazers.

The presence of a DCM around 40 m depth suggests that the upper trap missed a part of the sinking material from the euphotic zone. It may partially explain why the lower trap measured greater fluxes of BSi and pigments. Also, due to its position close to the surface, the current was tilting the surface trap, possibly reducing its trapping efficiency.

Lateral advection of particles has already been suggested to be important in the GSL (Savenkoff *et al.*, 1996). Depth-averaged (integrated between 0-20 m and 0-100 m) residual current velocities in the study area typically varied between 5 cm s⁻¹ from spring to autumn and 25 cm s⁻¹ during winter (Galbraith *et al.*, 2015, 2016). This may lead to horizontal drifts ranging from 4.3 to 21.6 km d⁻¹ (approximately 6.5 km d⁻¹ during the peak in POC flux). Furthermore, the surface geostrophic currents in the Cabot Strait region are changing seasonally (El-Sabh, 1976; Galbraith *et al.*, 2015, 2016), therefore influencing the origin of the material collected in the traps. The station was influenced at both depths by inflowing surface Atlantic water from October 2014 to March 2015, whereas by a mix of this water and outflowing surface GSL water from April to July 2015 (Galbraith *et al.*, 2015, 2016). For protists sinking slowly, e.g. diatoms and dinoflagellates, lateral advection may have been of great importance. Diatoms typically sink at speeds of <1 to 10 m d⁻¹ but sometimes as much as 30 to 50 m d⁻¹ in bloom conditions (Turner, 2002). Based on the calculations of Bach *et al.* (2012) for estimating sinking velocities, and considering an equivalent spherical diameter of 130 µm, we estimated that *Protoperidinium* spp. sank at velocities of about 8 m d⁻¹. Assuming for the calculations, that the cells started to sink from the surface, the residence time of diatoms in the upper 100 m ranged from 10 to >100 d (2 to 3 d in bloom conditions) while the residence time of dinoflagellates was about 12.5 d. Thus, by multiplying daily horizontal drift by residence time in the upper 100 m of the water column, diatoms and dinoflagellates collected at 100 m originated from 43 to >2160 km (13 to 22 km during the peak) and from 54 to 270 km, respectively. Due to a shorter residence time of cells in the upper 34 m compared to the upper 100 m, horizontal drift may have been of smaller importance at the upper trap, resulting in a more distant origin of the sinking particles at 100 m. This estimation does not consider the possible importance of vertical mixing observed by Stukel and Ducklow (2017). Vertical mixing would be most important in winter, when thermal stratification is minimal and could lower the residence time of cells by exporting them out of surface waters. Lateral advection may have been of

great importance as well for protists capable of remaining at a specific depth or swimming (i.e. foraminifera and dinoflagellates) because it may extend their residence time in the upper water column. Fairbanks *et al.* (1980) reported that foraminifera showed species-specific vertical distribution patterns in the NW Atlantic. In his study, Bé (1977) classified some species based on their vertical distributions. Several species present on the Scotian Shelf (Bé, 1959; i.e. *Globigerina bulloides*, *Orbulina universa*, *Hastigerina pelagica*, *Globigerinella aequilateralis*, *Globigerinita glutinata*) were classified in Bé's intermediate water depth assemblage and would live predominantly between 50 and 100 m depth. Dinoflagellates, dominated by the genus *Protoperidinium*, appeared to be located mostly above 34 m during the end of winter and spring. Swimming and vertical migration behavior are known features of some dinoflagellate species (Eppley *et al.*, 1986; Smayda, 2000, 2010; Jephson 2012). Thus, we believe that *Protoperidinium* spp. found in this study may possibly show these behaviors as well.

Active transport may have been an important mechanism influencing fecal pellet related fluxes. Vézina *et al.* (2000), based on several stations of the Canadian JGOFS dataset, calculated that active transport represented between one-half and one-third of the particle flux. Angel (1984) discussed the possible importance of defecation at depth in zooplankton based on the gut retention time in various planktonic organisms. He summarized that if the retention time was long enough for an animal feeding near the surface to migrate down the water column with a full gut, DVM would possibly play an important role in transport of organic carbon at depth. Roy *et al.* (2000a) and Harvey *et al.* (2009) showed the importance of DVM for several species of zooplankton in the GSL. Simard *et al.* (1985) showed the importance of that process for *C. finmarchicus*. That species showed a bimodal twilight grazing rhythm, feeding above 30 m depth and migrating below, mostly with a gut containing pigments. By doing so, *C. finmarchicus* may release more fecal pellets to depth than near the surface. Containing POC and seasonally, the phytoplanktonic remains of their diet, i.e. pigments and BSi (Schrader, 1971; Bathmann

and Liebezeit, 1986; Roy *et al.*, 2000a; Reigstad *et al.*, 2005), active transport of fecal pellets may have contributed to the observed differences in magnitude of the latter fluxes. We believe that the higher values of POC at 34 m around the bloom are due to higher debris proportion and more heterotrophic origin of the sinking material (e.g. heterotrophic dinoflagellates and zooplankton appendages). The augmentation of FPC fluxes with depth suggests, on the opposite of the previous CJGOFS studies in the GSL, that recycling of FPC was less important than active transport in this study. Roy *et al.* (2000a) observed decreasing FPC fluxes and fecal pellet contributions in spring, summer and autumn between 50 m and 150 m. A model developed by Tian *et al.* (2000), showed that the sinking flux of particles declined, but very little between 50 m and 100 m. Thus, it seems possible that most of the recycling of FPC in the GSL happens below 100 m depth.

We believe that active transport of particulate matter by *C. finmarchicus* and other zooplankters and the position of the upper trap above the DCM are the main causes for the differences observed in terms of magnitude of BSi and pigments fluxes between depths. Active transport also accounts for differences in FPC contributions. Lateral advection of adjacent waters (i.e. inflowing Atlantic waters or outflowing GSL waters) better explain the differences in protist community composition between both depths. Cells characterized by a long residence the upper water column (e.g. Ribbon spp., *O. aurita*, *Chaetoceros* spp., dinoflagellates and foraminifera) are the most subject to transport through currents.

2.4.5. Comparison with earlier GSL measurements

Peak and annual POC fluxes values measured in this study were very low compared to previous studies realized in the GSL under the Canadian JGOFS program (Table 2). Using drifting sediment traps, Rivkin *et al.* (1996) and Romero *et al.* (2000) measured peak values up to ten-fold higher and annual values up to 40 times higher than in this study. We believe that the location of our station, affected by the seasonal influence of inflowing

oligotrophic Atlantic waters is the major explanation of the differences of magnitude observed between studies.

The great difference of magnitude observed between the bloom period and the rest of the year in our study also contrasts with JGOFS results. Rivkin *et al.* (1996) showed that while both food-web structure and new production estimates were different during (April) and after the spring phytoplankton bloom (June) in 1994 in the GSL, the biogenic carbon flux—as estimated using shallow surface-tethered sediment traps—was similar for the two periods. Based on these observations, they argued that there was no food-web control over the intensity of POC fluxes. We believe that several factors led to the differences observed between both studies. First, their sampling stations were located in the western part of the GSL, a region more productive than the Cabot Strait region. Second, as argued by Vézina *et al.* (2000) and Romero-Ibarra and Silverberg (2011), the use of drifting sediment traps during a short period of time (i.e. 24 h) may possibly lead to miss a punctual event such as a spring pulse of flux. Rivkin *et al.* (1996) considered their results representative of the sampled periods (bloom and post-bloom). Our moored traps measured the flux constantly during the sampling year, catching the whole spectrum of each period. Finally, the bloom fluxes presented by Rivkin *et al.* (1996) were measured under variable ice cover conditions (up to 100% ice cover; Savenkoff *et al.*, 2000). As in this study and in the model developed by Le Fouest *et al.* (2005), the phytoplankton bloom in the GSL generally occurs after the retreat of sea ice. Therefore, Rivkin *et al.* (1996) may have missed the spring bloom at most of their stations; their sampling occurring most probably before the bloom (see Savenkoff *et al.*, 2000). We believe that the bloom conditions and associated fluxes presented in their paper are not representative of bloom conditions in the GSL. In our view, this is the main reason why their bloom and post-bloom periods show similar magnitudes of fluxes, although the arguments discussed in Boyd *et al.* (1997) may also have played a role.

During the second half of June 2015, we measured a POC flux of $3.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 100 m, which is approximately 5 times lower than the value of $16 \text{ mg C m}^{-2} \text{ d}^{-1}$ measured by Romero *et al.* (2000) on 25 June 1994 in Cabot Strait. They sampled a station located 51 km south of our sampling location by deploying a drifting sediment trap for 24 h at 150 m depth. We suspect that the large difference observed is mainly due to the surface circulation pattern in Cabot Strait (El-Sabh, 1976; Galbraith *et al.*, 2015, 2016). Our traps were probably collecting materials originating from a mix of inflowing surface Atlantic waters and of outflowing GSL waters. On the other hand, the trap of Romero *et al.* (2000) in June was probably trapping materials from the GSL outflow. The consistent presence of planktonic foraminifera in our trap at 100 m over the study period seems to support this hypothesis.

2.5. CONCLUSION

The annual cycle of POC flux in the GSL was characterized by a short, marked peak of POC around the spring bloom and by much lower values the rest of the year. The varying composition of sinking material throughout the year showed an important planktonic succession through the seasons. POC fluxes at the study location were low in comparison with other subarctic areas and previous studies in the GSL. The oligotrophic character of the sampling station, due to inflowing Atlantic waters through Cabot Strait, could be an explanation for those discrepancies. Lateral advection and active transport were two important mechanisms in this study, contributing greatly to the observed magnitudes and composition of the fluxes. In order to better assess the link between the vertical fluxes and the oceanographic conditions, future studies should focus on measuring more accurately and more regularly biological water conditions (e.g. POC and chlorophyll *a* concentrations, phyto- and zooplankton abundances). This may be done by coordinating the mooring of traps with water samplings at the position of the moorings several times during the sampling period. Moorings could also include fluorescence probes placed at several

depths in order to follow the evolution of chlorophyll *a* concentration in the water column. This study reminds the need to place more effort on survey programs. Further work needs to be done on different plankton taxa such as foraminifera, dinoflagellates, tintinnids, pteropods, hyperiids and chaetognaths, which contributions were considerable in the swimmer community or in the sinking material during the present study. Those taxa participated significantly in the POC fluxes at specific periods of the year, including during the peak of sinking carbon.

2.6. ACKNOWLEDGEMENTS

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3. CONCLUSION GÉNÉRALE

Cette étude présente la première série annuelle complète de flux verticaux dans le GSL. Les mesures effectuées apportent ainsi des données inédites et essentielles pour la compréhension des flux verticaux et de l'écosystème du GSL. Ils donnent également un aperçu unique sur la saisonnalité de l'écosystème planctonique dans le GSL. Ces résultats s'inscrivent d'une part dans une volonté de mieux caractériser l'écosystème du GSL et d'autre part dans une volonté de davantage caractériser les flux en milieux côtiers afin de les intégrer dans les modèles globaux.

Le GSL est l'objet de suivis réguliers par le ministère de Pêches et Océans Canada (MPO) mais aussi par des universités canadiennes et des institutions privées. Les études réalisées sont des pas importants vers la compréhension de sa complexité et aussi une façon de suivre son évolution dans un contexte de changement climatique. Bien que certains aspects soient fortement suivis, d'autres restent encore pleinement à découvrir. La présente étude en est un exemple car ces résultats font émerger plus de nouvelles questions sur la dynamique de l'écosystème planctonique et leur influence sur les flux biogéochimiques qu'ils n'apportent de réponses.

Les écosystèmes côtiers sont souvent sous-évalués dans les modèles globaux d'évaluation des flux verticaux de carbone. Le GSL doit continuer d'être caractérisé de différentes façons afin d'apporter une validité croissante aux modèles d'évaluation des flux verticaux de carbone à échelle régionale et globale. Bien que cette étude ait été réalisée une vingtaine d'années après l'échantillonnage du programme canadien du JGOFS et présente des flux de COP fort différents, nous ne pensons pas que les changements climatiques en soient responsables. La nature oligotrophe de la station est probablement la principale cause des différences observées. Cependant, nous pensons qu'il est indispensable de suivre son éventuelle réponse aux changements climatiques.

Lors du programme canadien du JGOFS, le déploiement des pièges à particules avait occasionné la mesure d'autres variables de la colonne d'eau. La présente étude aurait certainement eu à gagner de pouvoir davantage lier les flux verticaux et la nature du matériel particulaire aux conditions physiques et biologiques de la colonne d'eau. Outre les échantillonnages ponctuels de chlorophylle *a in situ* à proximité du mouillage, aucune donnée physique et biologique n'a été récoltée durant cette étude. Nous pensons que de futures études auraient tout intérêt à coordonner leur échantillonnage avec les suivis réguliers effectués par le MPO afin que des liens puissent être trouvés entre les conditions *in situ* et le matériel observé dans les pièges à particules. Une évaluation simultanée des flux et des communautés bactérienne, phytoplanctonique et zooplanctonique présentes dans la colonne d'eau, apporterait certainement de nouvelles perspectives aux futures études. Au minimum, il serait intéressant d'installer des sondes de salinité, de température et de fluorescence *in vivo* sur le mouillage, couvrant l'ensemble de la zone euphotique.

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5. ANNEXES

Annex 1. Biovolume to carbon conversion factors of the different types of identified particles. Carbon biomass (C) is expressed in pg and biovolume (V) in μm^3 in the equations

Type	Conversion factor	Reference
Diatoms < 3000 μm^3	$C = 10^{(-0.541 + 0.811 \times \log(V))}$	Menden-Deuer and Lessard (2000)
Diatoms > 3000 μm^3	$C = 10^{(-0.933 + 0.881 \times \log(V))}$	Menden-Deuer and Lessard (2000)
<i>Chaetoceros</i> spores	$C = 0.473 \times V$	Kuwata et al. (1993)
Thecate dinoflagellates	$C = 10^{(0.175 + 0.764 \times \log(V))}$	Menden-Deuer and Lessard (2000)
Unidentified dinoflagellates	$C = 10^{(-0.353 + 0.864 \times \log(V))}$	Menden-Deuer and Lessard (2000)
Coccolithophorids	$C = 10^{(-0.642 + 0.899 \times \log(V))}$	Menden-Deuer and Lessard (2000)
Foraminifera	$C = 0.4 \times 0.2 \times V$	Silver and Gowing (1991)
Pollens	Assumed equivalent to diatoms < 3000 μm^3	Romero-Ibarra and Silverberg (2011)
Cylindrical pellets	$C = 0.030 \times V$ in spring, summer and beginning of autumn $C = 0.018 \times V$ in autumn and winter	Manno et al. (2015)
Ovoid pellets	$C = 0.052 \times V$ in spring, summer and beginning of autumn $C = 0.034 \times V$ in autumn and winter	Manno et al. (2015)
Broken pellets	$C = 0.041 \times V$ in spring, summer and beginning of autumn $C = 0.026 \times V$ in autumn and winter	Mean of ovoid and cylindrical pellets

Annex 2. The ratio of POC to pigments (in g:g) in the sinking material and the percent contribution of protists plus fecal pellets carbon to the sinking POC. Sampling periods are indicated in Table 1. n.d.: no data

Sample cup	POC:pigments		%POC	
	34 m	100 m	34 m	100 m
/				
1	n.d.	1948	n.d.	83
2	n.d.	1193	n.d.	21
3	740	588	25	16
4	n.d.	291	n.d.	68
5	465	53	n.d.	138
6	191	209	206	71
7	107	82	172	106
8	668	66	172	90
9	1560	107	27	81
10	63	8	17	104
11	440	9	8	144
12	7227	19	22	161
13	317	20	31	131
14	357	27	9	45
15	115	46	73	26
16	41	809	115	74
17	127	1385	61	157
18	n.d.	1818	n.d.	154
19	n.d.	2079	n.d.	168
20	n.d.	1996	n.d.	60
21	n.d.	3595	n.d.	7
22	n.d.	3616	n.d.	26
23	n.d.	1512	n.d.	24
24	n.d.	2197	n.d.	7