Migration verticale du zooplancton et flux respiratoire de carbone en mer de Beaufort (Arctique canadien)

Thèse

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Résumé

Le zooplancton exerce un rôle primordial dans les transferts d'énergie à travers les réseaux trophiques océaniques et dans le cycle biogéochimique du carbone des écosystèmes marins. La communauté entière recycle du CO_2 en consommant le carbone photosynthétiquement fixé en surface, et en le respirant ensuite. Des migrateurs verticaux transportent du carbone stocké et le respirent en profondeur, contribuant à son exportation de la zone épipélagique. En Arctique, ce flux actif respiratoire n'a pas été mesuré, malgré un potentiel élevé de transport du à la forte contribution du migrateur saisonnier *Calanus hyperboreus* à la biomasse zooplanctonique. Cette thèse exploite une série quasi-annuelle de profils de biomasse et de respiration zooplanctoniques pour : (1) quantifier ce processus en mer de Beaufort; (2) améliorer les connaissances sur les fluctuations saisonnières de la distribution verticale de sept copépodes arctiques clés; et (3) suivre le cycle biologique de *C. hyperboreus*. Ce grand herbivore constituait 45 % de la biomasse zooplanctonique et a effectué les migrations verticales les plus extensives. Son ascension saisonnière, de l'ordre de 200 m, et celles de moindre ampleur de *C. glacialis* et du petit omnivore *Oithona similis*, ont coïncidé avec les efflorescences d'algues de glace et phytoplanctoniques. Malgré une reproduction hivernale vigoureuse en profondeur, une débâcle hâtive de la banquise, et une production primaire élevée, un faible recrutement au stade copépodite a entrainé une stagnation de la croissance de la population de *C. hyperboreus*. Très abondant, l'omnivore *Metridia longa*, et *Microcalanus pygmaeus*, ont pu exercer dans leur habitat mésopélagique un contrôle sur cette population en interceptant les œufs de *C. hyperboreus* flottant vers la surface. Le cryophile *Pseudocalanus* spp. est resté en permanence dans la zone épipélagique froide, tandis que le mésopélagique *Triconia borealis,* possiblement un semi-parasite de *C. hyperboreus,* était associé avec dans la couche Atlantique plus chaude. La température a eu peu d'effet sur les déplacements verticaux des copépodes arctiques. Le grand zooplancton, dominé par les *Calanus*, était responsable de 89% du broutage zooplanctonique de la production primaire brute d'avril à juillet. Les transports de carbone au delà de 100 m et 200 m par ces *Calanus* étaient du même ordre de grandeur que les flux gravitationnels de carbone organique particulaire à ces profondeurs. Ces résultats soulignent l'importance d'inclure le transport actif dû aux migrateurs saisonniers du grand zooplancton dans les bilans de carbone de l'Océan Arctique.

Abstract

Zooplankton play a pivotal role in the energy transfer through the oceanic food webs and in the biogeochemical carbon cycle within marine ecosystems. The entire community recycles CO_2 by consuming photosynthetically fixed carbon and respiring it thereafter. Vertical migrants transport stored carbon and respire it at depth, thus, contributing to its export from the epipelagic zone. Active respiratory flux has not been measured in the Arctic despite the high potential for transport due to the strong contribution of the seasonal migrant *Calanus hyperboreus* to zooplankton biomass. This thesis exploits a quasi-annual time series of zooplankton biomass and respiration profiles to: (1) quantify this process in the Beaufort Sea; (2) improve our knowledge on the seasonal fluctuations of the vertical distribution of seven key arctic copepods; and (3) track the life cycle of *Calanus hyperboreus*. This large herbivore contributed 45% to the zooplankton biomass and performed the most extensive vertical migration. Its seasonal ascent, ranging about 200 m, and those of lesser magnitude of *C. glacialis* and the small omnivore *Oithona similis*, coincided with the ice algae and phytoplankton blooms. Despite vigorous winter reproduction at depth, a precocious ice break-up, and high spring-summer primary production, weak recruitment to copepodite stage caused *C. hyperboreus* population growth to stagnate. In their mesopelagic habitat, the highly abundant omnivore *Metridia longa*, and *Microcalanus pygmaeus*, could have exerted a control on this population by intercepting *C. hyperboreus* eggs floating toward the surface. The cryophilic *Pseudocalanus* spp. remained year-round in the cold epipelagic zone while the mesopelagic *Triconia borealis*, likely a semi-parasite of *C. hyperboreus*, was associated with it in the warmer Atlantic layer. Temperature had little effect on the vertical displacements of arctic copepods. The *Calanus*-dominated large zooplankton was responsible for 89% of zooplankton grazing on the April-July gross primary production. Carbon transport below 100 m and 200 m depth, mediated by the *Calanus* species, was of the same magnitude as the gravitational fluxes of particulate organic carbon to these depths. These results stress the importance of including active transport by large zooplankton migrants in carbon budgets of the Arctic Ocean.

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Manniè tanbou-a ka woulé Menm manniè lanmè pé lévé

À la mémoire de mon père qui m’a transmis l’amour de la mer.

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Avant-propos

Cette thèse de doctorat en océanographie comporte cinq chapitres : une introduction générale (chapitre 1), une conclusion générale (chapitre 5), ainsi que trois chapitres (2 à 4) constituant le corps de la thèse et rédigés en anglais sous forme d'articles scientifiques dont voici les références:

Chapitre 2 : **Darnis**, G. Fortier, L. Food, temperature, and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean)

Chapitre 3 : **Darnis**, G. Wold, A. Falk-Petersen, S. Fortier, L. Life strategy and reproduction of the arctic copepod *Calanus hyperboreus* during a year of record-low ice cover in the southeastern Beaufort Sea. Ce chapitre sera bientôt soumis à Marine Biology.

Chapitre 4 : **Darnis**, G. Fortier, L. (2012) Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean). J. Geophys. Res., 117, C04013 (article reproduit avec l'autorisation de l'éditeur).

J'ai conçu ce projet de recherche, organisé l'échantillonnage et les expériences en mer, participé à une grande partie des missions océanographiques du projet pluridisciplinaire Circumpolar Flaw System Study (CFL), réalisé les analyses en laboratoire, et supervisé un stage de master français et une initiation à la recherche en lien avec ma recherche doctorale. J'ai de plus réalisé l'ensemble des analyses statistiques, puis rédigé les différents chapitres avec l'aide de mon directeur de thèse Louis Fortier, et de mes coauteurs du chapitre 3, Anette Wold et Stig Falk-Petersen.

Les résultats issus de ces travaux de recherche ont également fait l'objet de communications scientifiques lors d'ateliers de travail et de congrès nationaux et internationaux :

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Forest, A., Galindo, V., **Darnis, G.**, Pineault, S., Lalande, C., Tremblay, J.-É., Fortier, L. 2011. Carbon biomass, elemental ratios (C:N) and stable isotopic composition (δ13C, δ15N) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). Journal of Plankton Research 33: 161-178 doi 10.1093/plankt/fbq103.

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Tremblay, J.-É., Robert, D., Varela, D.E., Lovejoy, C., **Darnis, G.**, Nelson, R.J., Sastri, A.R. 2012. Current state and trends in Canadian Arctic marine ecosystems: I. Primary production. Climatic Change. doi 10.1007/s10584-012-0496-3

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1. Chapitre 1 - Introduction générale

1.1 Le rôle des océans dans le cycle global du carbone

Les océans mondiaux constituent des réservoirs gigantesques de carbone qui, lors des échanges gazeux rapides et intenses avec l'air, influencent considérablement la teneur en dioxyde de carbone (CO_2) atmosphérique (Libes 2009). À ce jour, l'Océan global aurait absorbé près du tiers du carbone provenant des émissions atmosphériques dues aux activités de notre ère industrielle, au premier rang desquelles nous trouvons la combustion de sources d'énergie fossile, la déforestation et la production de ciment (Marinov et Sarmiento 2004). En détenant ce rôle primordial de puits dans le cycle global du carbone, l'Océan global contrôle dans une certaine limite le réchauffement climatique en tempérant l'effet de serre produit par l'accroissement rapide de la concentration de CO_2 d'origine anthropique (Jacques et Saugier 2008).

Le sens des échanges gazeux à l'interface entre l'air et la surface des océans connait des variations géographiques et saisonnières liées à des différences de pression partielle en CO_2 (ρCO_2) pouvant prendre des valeurs comprises entre 150 et 550 µatm dans la couche de mélange des eaux de surface (Takahashi et al. 2002b). Ainsi, par équilibration, un flux net positif de CO_2 s'effectue entre des eaux sous-saturées en ce gaz par rapport à l'atmosphère (395 µatm au début de 2013; Tans et Keeling 2013), faisant de ces régions des puits potentiels de carbone. De telles zones de prise de CO_2 atmosphérique se retrouvent dans les eaux froides de l'Atlantique et du Pacifique nord et de l'Océan austral où se forment les eaux profondes lors des processus de convection (Takahashi et al. 2002b). Un autre exemple marquant de puits de carbone est l'Océan Arctique, responsable de 5 à 14% de l'absorption océanique globale de CO_2 alors qu'il ne représente que 3,9% de la surface totale des océans (Bates et Mathis 2009; Bates et al. 2011). En revanche, les régions sursaturées en CO_2 comme le Pacifique équatorial, ou encore des zones localisées de remontée (upwelling) d'eaux profondes enrichies en CO_2 constituent des sources de carbone pour l'atmosphère.

Dans la couche de mélange des eaux de surface où les échanges avec l'atmosphère ont lieu, la ρCO_2 est influencée par des changements de température, la concentration totale en CO_2 et l'alcalinité (Volk et Hoffert 1985). Les variations de température sont généralement le fait de processus physiques comme l'insolation, les échanges de chaleur et l'épaisseur de la couche de mélange, alors que la concentration en CO_2 et l'alcalinité sont principalement régulées par des processus biologiques (photosynthèse, respiration et calcification) ou par la remontée d'eaux profondes (Libes 2009). Afin que persiste un déséquilibre de ρCO_2 favorable à la captation du CO_2 par l'océan, des mécanismes physiques et biologiques complexes doivent assurer une exportation vers les grandes profondeurs, et éventuellement vers le plancher océanique, du carbone fixé en surface. Dans ces zones, le carbone pourra être piégé hors de l'atmosphère pendant des périodes plus ou moins longues, et on parlera alors de séquestration du CO_2 si ce stockage se prolonge sur quelques centaines à des milliers d'années. Trois mécanismes, qualifiés de pompes à carbone, assurent le transport de carbone dans les couches profondes de l'océan : 1) la pompe de solubilité, 2) la pompe à carbonate, et 3) la pompe biologique (Volk et Hoffert 1985).

La pompe de solubilité est basée sur le fait que, en adéquation avec la loi des solutions diluées (dite loi de Henry), la solubilité du CO_2 augmente avec la baisse de température de l'eau et aussi avec une augmentation de la salinité (Marinov et Sarmiento 2004). Les eaux froides profondes devraient donc contenir plus de carbone inorganique dissous (CID = $CO_2 + HCO_3^- + CO_3^{2-}$) que les eaux de surface plus chaudes. Aux hautes latitudes de l'Atlantique nord et de l'Océan Austral, zones où la convection thermohaline forme les Eau Profonde Nord-Atlantique (EPNA) et Eaux Antarctique de Fond, des eaux de surface froides riches en CID plongent vers les profondeurs. Ainsi, l'EPNA atteint des profondeurs comprises entre 1500 et 2500 m et, en se déplaçant vers le sud, alimente la circulation thermohaline profonde (Broecker 1991). Cette dernière ayant un cycle d'à peu près mille ans, le carbone transporté d'abord en profondeur, puis avec la circulation profonde, est piégé à long terme.

Le fonctionnement de la pompe à carbonate est alimenté par la formation et la dissolution de calcite et d'aragonite, constituants des coquilles et d'exosquelettes d'organismes planctoniques tels que les coccolithophores, les foraminifères et dans une moindre mesure les mollusques ptéropodes (Fabry 1990; Iglesias-Rodríguez et al. 2002). Ces structures solides de carbonate de calcium ($CaCO_3$), souvent produites dans la couche de surface et plus denses que l'eau, peuvent sédimenter jusqu'à atteindre le fond, ou bien se dissolvent dans les eaux profondes aux conditions généralement plus acides (Volk et Hoffert 1985). L'amplitude du transport vertical de carbone par la pompe à carbonate dépend donc du pH des masses d'eau.

À la base de la pompe biologique, il y a l'utilisation du CO_2 par les producteurs primaires océaniques pour produire du carbone organique particulaire (COP) et de l'oxygène lors de la photosynthèse dans la zone euphotique. La majorité de ce COP est reminéralisée par la respiration dans la couche épipélagique. Le COP résiduel sera exporté de cette zone en étant entrainé sous la pycnocline par deux processus principaux : la sédimentation d'agrégats biogènes ballastés par des particules plus denses, et le transport actif sous la médiation du zooplancton (Honjo et al. 2008).

Ces processus sont détaillés dans les prochaines sections. Une partie du COP exporté sera reminéralisée par la respiration planctonique dans les profondeurs formant un premier niveau de séquestration. Le métabolisme planctonique laisse généralement peu de carbone organique de la production primaire nette atteindre le plancher océanique (De La Rocha et Passow 2007). À la fin de la sédimentation, la maigre fraction du carbone (1-3%), initialement fixé par la photosynthèse, alimentera soit la demande en carbone des organismes benthiques (Grebmeier et Barry 1991), soit le processus de séquestration de ce carbone dans les sédiments pour des millénaires (Honjo 2009).

1.2 Fonctionnement de la pompe biologique de CO_2

Pour expliquer la prise en charge et la séquestration de CO_2, le concept de pompe biologique mobilise de multiples composantes de l'écosystème pélagique, dont la disponibilité en nutriments inorganiques (nitrate, phosphate, silice et fer), les processus de photosynthèse, respiration, trophodynamiques, sédimentation, transport par les migrations du zooplancton ainsi que d'autres processus sous leur médiation (Longhurst et Harrison 1989; Honjo 2009). De plus, le fait que la pompe à carbonate, à l'origine de la formation de carbone inorganique particulaire, soit initiée par des processus biologiques est un argument pour la considérer comme une sous-composante de la pompe biologique (Jacques et Saugier 2008). Cette dernière est donc un système hautement complexe dont la compréhension du fonctionnement bénéficie d'une approche pluridisciplinaire à la base de la biogéochimie moderne.

La recherche actuelle sur les mécanismes de la pompe biologique s'appuie sur les travaux fondateurs de Dugdale et Goering (1967) qui ont formulé le concept de production primaire nouvelle/production régénérée. La production nouvelle est définie comme la fraction de la production primaire totale dans la zone euphotique soutenue par l'apport de sels nutritifs inorganiques en provenance des eaux profondes, des cours d'eaux et de l'atmosphère. Par contraste, la production régénérée est élaborée à partir des nutriments azotés tels que l'ammonium et l'urée, issus des processus métaboliques *in situ*. Autre contribution majeure à l'étude de la pompe biologique, Eppley et Peterson (1979) ont appliqué le concept de production nouvelle/production régénérée pour démontrer que cette fraction de la production primaire totale qu'est la production nouvelle (le facteur-f) définit la part du carbone organique biogène exportable du système épipélagique et qui sera à la base du flux de carbone vers l'intérieur de l'océan. Dans les zones océaniques relativement peu influencées par les apports latéraux de matière organique particulaire, ce lien étroit entre les taux d'exportation de COP et de production de particules biogènes à la surface est maintenant clairement reconnu (Deuser et al. 1981; Asper et al. 1992; Lalande et al. 2009a). Le flux vertical de carbone est ainsi influencé par les variations saisonnières de la production primaire pélagique, et aussi par la succession d'espèces au sein des communautés d'autotrophes au fil de la saison de production (Wassmann 1998; Sampei et al. 2002; Forest et al. 2008). Par exemple, les diatomées, qui dominent en début de cycle de production à des concentrations de nitrate plus élevées dans la couche de mélange, tendent à mieux alimenter un réseau trophique pélagique tourné vers l'exportation de carbone qu'un assemblage dominé par les flagellées (Wassmann 1998).

Mais la régulation du flux vertical de carbone est aussi en grande partie le fait d'un ensemble varié de processus liés aux communautés d'hétérotrophes planctoniques, et en particulier le zooplancton (Wassmann 1998). D'un côté, l'interception des particules, la dégradation des agrégats de matière organique particulaire, et ensuite la reminéralisation du carbone par la respiration en surface ou à différents niveaux de la colonne d'eau, favorisent le recyclage de CO_2 au détriment de l'efficacité de la pompe biologique. D'un autre côté, la production de résidus denses de la digestion qui accélèrent le flux gravitationnel de carbone, et le transfert de carbone de la surface vers les profondeurs par les migrations verticales du zooplancton qui induisent un flux actif de carbone, accroissent l'efficacité de la pompe biologique (Honjo et al. 2008).

1.3 Rôle du zooplancton dans le flux gravitationnel (passif) de carbone

Le flux gravitationnel de carbone est sans aucun doute le mécanisme d'exportation de carbone particulaire le mieux documenté. Depuis le début des années 1980, son étude bénéficie d'un réseau de pièges à particules étendu à travers la plupart des océans (Honjo 2009). Cela inclue également des régions arctiques telles que la mer de Beaufort (Forest et al. 2007; Forest et al. 2008; Sampei et al. 2009a; Sampei et al. 2011; Sampei et al. 2012), l'Arctique central (Honjo et al. 2010) la polynie des Eaux du Nord (Sampei et al. 2002; Sampei et al. 2004) et la polynie des Eaux du Nord-Est (Bauerfeind et al. 1997), la mer de Laptev (Lalande et al. 2009b), le détroit de Fram (Bauerfeind et al. 2005; Lalande et al. 2011), et aussi la baie d'Hudson (Lalande et Fortier 2011). En interceptant le flux vertical de particules, ces pièges nous renseignent non seulement sur la quantité de COP chutant passivement vers le fond, mais aussi sur la composition des particules.

Les analyses de la composition des particules exportées mettent en exergue la contribution importante des pelotes fécales produites par le mésozooplancton au flux vertical passif (Dam et al. 1995b; Le Borgne et Rodier 1997). En reconditionnant de petites cellules algales non assimilées avec d'autres déchets de la digestion pouvant servir de ballast, les grands copépodes calanoïdes omnivores et herbivores, ainsi que les microphages planctoniques (appendiculaires, salpes et certains ptéropodes) fabriquent des pelotes fécales volumineuses et denses à vitesses de sédimentation élevées leur permettant d'atteindre de grandes profondeurs avant dégradation complète (Fortier et al. 1994; Lombard et al. 2010). En plus d'une descente rapide, les pelotes fécales des copépodes et de certains autres arthropodes sont enrobées d'une membrane péritrophique (Gauld 1957) leur conférant une relative protection contre le délitement par action mécanique ou par des microorganismes recycleurs. La chute de carcasses de zooplancton constitue un autre flux non négligeable de COP vers le fond de l'océan (Sampei et al. 2009b; Sampei et al. 2012). La prédation exercée par le zooplancton omnivore et carnivore sur les ciliées, les dinoflagellés hétérotrophes et le petit zooplancton détritivore réduit la pression de broutage sur la biomasse algale et les grosses pelotes fécales, et ainsi permet d'augmenter l'ampleur du flux de matière biogène sous la forme d'agrégats de cellules phytoplanctoniques et de détritus denses (Atkinson 1995; Wassmann 1998).

Dans des régions soutenant une biomasse planctonique élevée, un impact de broutage fort du zooplancton sur les stocks d'algues pélagiques divertit une portion du carbone photosynthétiquement fixé vers les niveaux trophiques supérieurs occupés par les vertébrés prédateurs (Figure 1.1) (Welch et al. 1992; Tremblay et al. 2006; Forest et al. 2011b). Ce transfert trophique généralement latéral de carbone diminue l'efficacité de la pompe biologique. Une fraction considérable du carbone ingéré et assimilé par les espèces zooplanctoniques est reminéralisée en CO_2 lors de la respiration (42-72%, cf. Ikeda 1985). Un tel recyclage dans le système épipélagique a pour effet d'augmenter la ρCO_2 à la surface et cette rétention de carbone réduit la capacité de l'océan à absorber du nouveau CO_2 atmosphérique. Par ailleurs, en interceptant le flux passif de matière détritique et en respirant par la suite ce carbone provenant de la surface, le zooplancton mésopélagique résident, à dominante détritivore et carnivore (Steinberg et al. 2008a), limite d'autant l'apport de COP au fond. Par leur alimentation, des espèces coprophages retirent des pelotes fécales du flux vertical alors que le zooplancton au complet participe à fragmenter les pelotes par simple manipulation ou contact (coprorhexie), avec pour effet potentiel de les rendre impropres à la sédimentation marine (Wassmann 1998). L'émiettement en particules plus petites lors de l'alimentation est accompagné de l'émission de carbone organique dissous qui pourra être recyclé en surface par la respiration bactérienne (Forest et al. 2011b). Les actions de coprophagie et de coprorhexie sont principalement le fait de petites espèces de copépodes (cyclopoïdes et poecilostomatoïdes) dominant nettement l'abondance zooplanctonique dans la plupart des systèmes épi-et mésopélagiques marins (Gonzalez et Smetacek 1994; Beaumont et al. 2001; Wexels Riser et al. 2002). De plus, ce petit zooplancton produit des pelotes fécales de petite taille, en grande partie

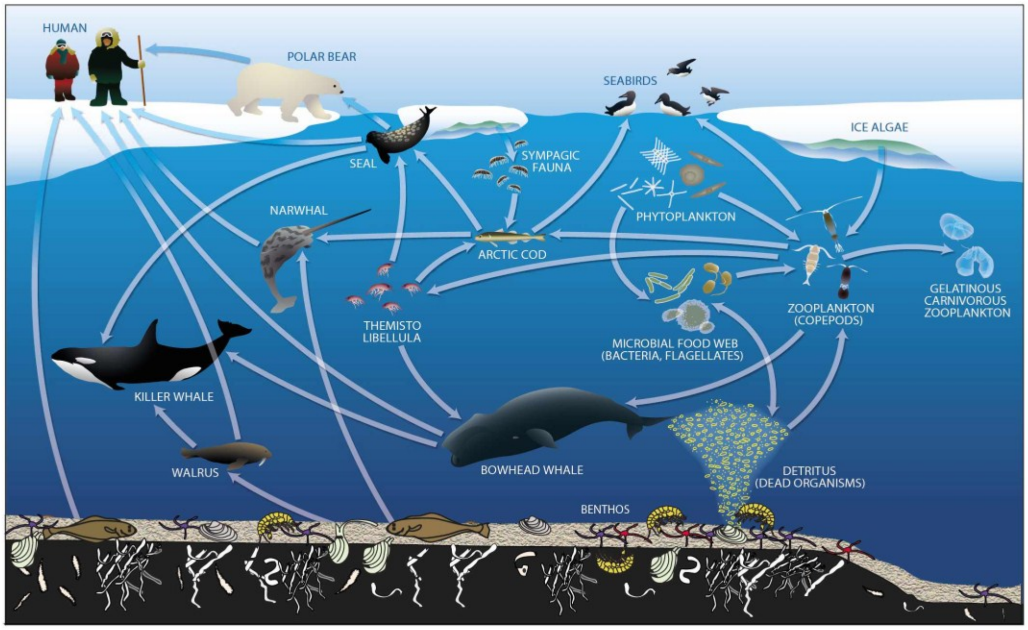


Figure 1.1. Représentation schématique du réseau trophique marin de l’Arctique canadien, avec une transition d’un écosystème côtier vers un océanique (gauche à droite). Graphique adapté de Darnis et al. (2012).

retenues dans le système épipélagique en raison de leur faible vitesse de sédimentation, et qui contribuent donc relativement peu au flux fécal de COP.

1.4 Rôle du zooplancton dans le flux actif de carbone

Les pièges à particules ne permettant pas de prendre en compte le transport actif de carbone dû aux déplacements des animaux dans la colonne d'eau, l'étude de cette composante de la pompe biologique a connu un développement plus tardif que celle du flux passif. Les premières estimations de ce flux, qui représentait 13-58% du flux passif de COP à des stations profondes de zones intertropicales, ont cependant vite démontré l'importance de ce processus pour l'exportation de carbone hors de la couche de surface (Longhurst et al. 1990). Des études plus récentes, citées par Kobari et al. (2008), ont même montré que dans certaines régions océaniques caractérisées par une forte biomasse de migrants verticaux, la quantité de carbone transportée activement au delà de 1000 m de profondeur pouvait dépasser de beaucoup le flux gravitationnel de COP, jusqu'à 145-340% de ce dernier.

1.4.1 Migrations verticales du zooplancton

Le transport actif de carbone est gouverné essentiellement par la migration verticale du zooplancton, et dans une moindre mesure par celle de certaines espèces de poisson faisant partie du micronecton (Vinogradov 1997; Angel et Pugh 2000). Dans le contexte de l'évaluation du rôle de ce processus dans la pompe biologique, deux catégories principales de migration sont reconnues chez le zooplancton : (1) la migration verticale nycthémérale (MVN) qui se déroule au cours d'un cycle approximatif de 24h00 et (2) la migration verticale saisonnière (MVS) qui est surtout, mais pas toujours, le fait d'espèces disposant d'une période de repos métabolique (diapause) dans leur cycle annuel (Johnson et al. 2006). Les causes fondamentales de ces comportements de migration ne sont, à ce jour, pas bien cernées et une chose sure est qu'elles sont diverses et sans doute d'importances variables. Certaines des hypothèses les plus communément avancées pour expliquer ces déplacements de zooplancton sont reprises par Fortier et al. (2001), qui traitent notamment de l'optimisation de l'environnement pour le métabolisme, l'évitement des prédateurs et des facteurs nocifs tels que le rayonnement UV. Nous pourrions aussi citer l'accès à des ressources pour des carnivores. L'ampleur de ces migrations est également très variable, de l'ordre de quelques mètres à plusieurs centaines de mètres, voire du kilomètre (Vinogradov 1997). Ce dernier point est d'une grande importance pour la séquestration du carbone car, pour que cette dernière se fasse, il faut que le carbone transporté soit au moins solubilisé sous une pycnocline permanente séparant la zone épipélagique des couches profondes (Longhurst et Harrison 1989).

Des études comparant des profiles de biomasse nocturnes et diurnes ont mis en évidence des déplacement journaliers sur plusieurs centaines de mètres chez des salpes, amphipodes euphausidés, chaetognathes, ptéropodes et grands copépodes (Longhurst et Harrison 1988; Lampitt et al. 1993; Vinogradov 1997; Angel et Pugh 2000; Madin et al. 2006; Takahashi et al. 2009). Les grands copépodes forment également le principal groupe à avoir des espèces impliquées dans des migrations saisonnières de grande amplitude (Hirche 1997; Bradford-Grieve et al. 2001; Kobari et al. 2003; Kobari et al. 2008). En revanche, les petites espèces de copépodes comme *Oithona* sp. et les Oncaeidés, souvent omnivores et cryptiques, ne sont pas reconnues pour se déplacer verticalement sur de longues distances (Vinogradov 1997). Longhurst et Harrison (1988) considèrent qu'à l'échelle globale, 15 à 50% de la biomasse de zooplancton métazoaire comprise dans les 500 premiers mètres de la colonne d'eau, se déplace la nuit vers la surface pour se nourrir. Une estimation globale de l'ampleur de la translocation verticale de biomasse zooplanctonique par la migration saisonnière ne semble pas avoir été faite. Cependant, des mesures régionales indiquent qu'elle peut être considérable où le zooplancton est dominé par des migrateurs saisonniers, à savoir les zones profondes de l'Atlantique nord, du Pacifique nord, de l'Océan Austral et de l'Océan Arctique. Par conséquent, l'étude de la fonction du zooplancton au sein de la pompe biologique dans un écosystème marin donné bénéficiera d'une description de la communauté en place, ainsi que des patrons de distribution verticale, la biomasse totale zooplanctonique seule n'étant pas un prédicteur suffisant du flux de carbone (Ducklow et al. 2001).

1.4.2 Modalités du flux actif

La première étape du flux actif est l'incorporation de carbone lors de l'alimentation dans le système épipélagique. Après la descente du zooplancton sous la pycnocline, une partie de ce carbone organique particulaire pourra être reminéralisée en CO_2 dans la couche mésopélagique et ainsi piégée jusqu'à la résurgence de ces eaux parfois après plusieurs siècles. Ce processus est qualifié de flux actif respiratoire. Mais, le flux actif de carbone inclue également la défécation en profondeur suite à une alimentation en surface (Hernández-León et al. 2001), l'excrétion de carbone organique dissous métabolisable par les communautés microbiennes profondes (Steinberg et al. 2000), la mue et la perte de biomasse migrante par la prédation et la mortalité naturelle en profondeur (Zhang et Dam 1997).

L'appréciation du rôle du transport actif dans l'exportation du carbone biogène se fait généralement en comparant la quantité de COP perdue par les migrateurs verticaux sous une profondeur donnée avec le flux gravitationnel atteignant celle-ci. Ainsi, le flux respiratoire imputable aux migrateurs nycthéméraux, dans différentes zones des Océans Atlantique et Pacifique à différentes périodes du cycle de production biologique, a été estimé à 3-72% du flux de COP mesuré à l'aide de pièges à particules (Tableau 1.1). Dans certaines situations, le flux actif respiratoire sur une période journalière peut donc être un processus valant la peine d'être comptabilisé dans le bilan de la pompe biologique.

Par contre, sur la base d'études réalisées dans le Nord Atlantique, Longhurst et Williams (1992) soutiennent que le rôle des migrateurs saisonniers dans le transport actif de carbone au cours de l'hivernage, est insignifiant (flux engendré par la perte de biomasse par mortalité <1% du flux passif) comparativement à celui des migrateurs nycthéméraux. Par la suite, Morales (1999) a révisé cette contribution de migrateurs saisonniers à la hausse mais celle-ci demeure faible pour la même région (3-4% des taux de sédimentation). D'un autre côté, le flux actif dû aux saisonniers peut être proche (73-92%) du flux gravitationnel de COP (Kobari et al. 2003; Kobari et al. 2008), voire le dépasser de beaucoup (260-340%; Bradford-Grieve et al. 2001) dans les mers subarctiques australes et nord-pacifique. Ce sont des régions où la biomasse zooplanctonique est particulièrement élevée et amplement dominée par les grands copépodes *Neocalanus* sp. et *Eucalanus* sp. qui hivernent à plusieurs centaines de mètres de profondeur. Manifestement, il faudrait plus d'études visant à quantifier le carbone perdu en profondeur par les migrateurs saisonniers si nous voulons clarifier à l'échelle globale leur rôle dans l'exportation de carbone particulaire. Ce type de travail requiert en premier lieu des séries temporelles de la biomasse migrante et de sa distribution verticale extrêmement difficiles à obtenir sur un laps de temps d'une année. Une autre tâche ardue est d'estimer la variabilité saisonnière des taux de respiration s'il s'agit de déterminer le flux actif respiratoire.

1.4.3 Mesure du flux actif dans les systèmes arctiques

À ma connaissance, aucune étude du genre n'a été menée dans les zones profondes des plateaux continentaux et les bassins océaniques de l'Océan Arctique, et cela en dépit du potentiel élevé d'exportation de carbone que les migrateurs saisonniers pourraient y avoir (Hirche 1997). En effet, ces écosystèmes pélagiques caractérisés par un régime de production primaire hautement saisonnier constituent l'habitat des grands copépodes herbivores *Calanus glacialis* et *C. hyperboreus*, y dominant la biomasse zooplanctonique et impliqués dans des migrations verticales saisonnières extensives (Hirche 1997; Vinogradov 1997; Ashjian et al. 2003; Auel et al. 2003). Dans son étude du cycle vital de *C. hyperboreus*, Hirche (1997) fait une estimation vague du carbone transporté par la migration descendante de cette espèce qui suggère effectivement que le flux actif sous sa médiation pourrait excéder le flux gravitationnel dans la mer du Groenland.

Tableau 1.1. Comparaison des flux actifs dus aux migrations verticales nycthémérales et saisonnières avec les flux passifs de carbone organique particulaire aux profondeurs propres à chacune des études menées dans des eaux océaniques profondes.

Région	Période	Taxon	Type du flux actif	Flux actif/flux passif (%)	Prof. (m)	Référence
MVN						
Atlant. subtropical	Sept	Méso+Macro	Resp.	4-14	150	Longhurst et al. (1990)
	Sept	Méso+Macro	Resp.	13-58	Pyc.	Longhurst et al. (1990)
Bermuda (BATS)	Mar-Avr	Méso	Resp.	18-70	150	Dam et al. (1995a)
	Année	Méso+Macro	Resp.	0-39	150	Steinberg et al. (2000)
Canary	Aout	Méso	Resp.	22-28	150	Hernández-León et al. (2001)
Pacif. équatorial	Mar-Avr	Méso	Resp.	18	150	Zhang et Dam (1997)
	Sep-Oct	Méso	Resp.	25	150	Zhang et Dam (1997)
	Sep-Oct	Méso+Macro	Resp.	8	150	Le Borgne et Rodier (1997)
	Sep-Oct	Méso+Macro	Resp.	4	150	Rodier et Le Borgne (1997)
Pacif. subtropical	Année	Méso+Macro	Resp.	12-18	150	Al-Mutairi et Landry (2001)
	Juin-Juil	Méso+Macro	Resp.	18	150	Steinberg et al. (2008b)
Pacif. Nord (Oyashio)	Aout	*Metridia pacifica*	Resp.	15	150	Takahashi et al. (2009)
Pacif. subarctique	Année	*Metridia pacifica*	Resp.	10	150	Kobari et al. (2008)
	Juil-Aout	Méso+Macro	Resp.	72	150	Steinberg et al. (2008b)
MVS						
Atlant. Nord	Année	Copépodes	Mort.	<1	200	Longhurst et Williams (1992)
Pacif. Nord	Année	*Neocalanus* spp.	Resp.+Mort.	91	1000	Kobari et al. (2003)
Pacif. subarctique	Année	*Neocalanus flemingeri*	Resp.+Mort.	9	1000	Kobari et al. (2008)
	Année	*N.cristatus ; N. plumchrus*	Resp.+Mort.	64	1000	Kobari et al. (2008)
	Année	*Neocalanus* spp.	Mort.	190	1000	Bradford-Grieve et al. (2001)
Pacif. sud subtropical	Année	*Neocalanus tonsus*	Mort.	262	1000	Bradford-Grieve et al. (2001)
Pacif. Sub-antarctique	Année	*Neocalanus tonsus*	Mort.	340	1000	Bradford-Grieve et al. (2001)

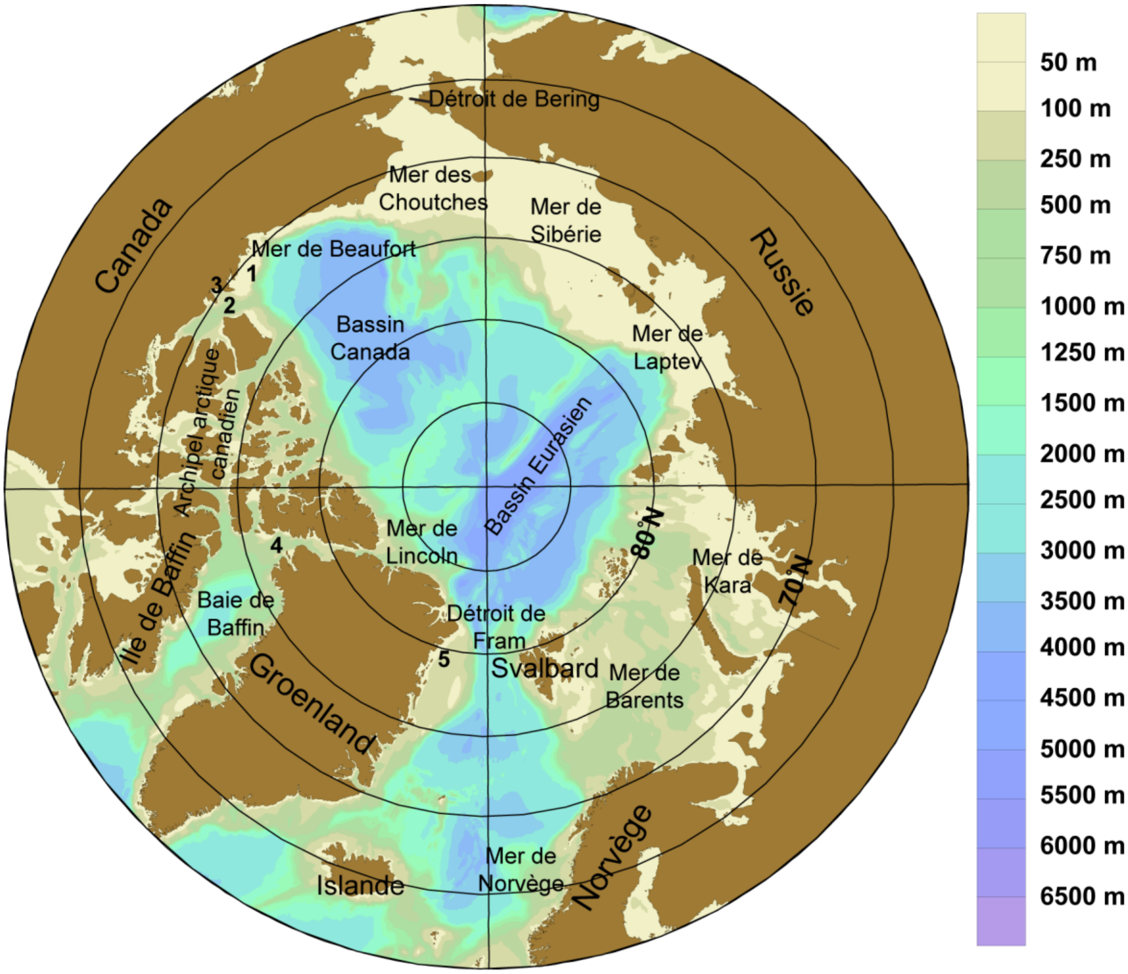
MVN, migration verticale nycthémérale; MVS, migration verticale saisonnière; Méso, mésozooplancton ; Macro, macrozooplancton ; Resp., transport actif du à la respiration en profondeur ; Mort., transport actif du à la mortalité en profondeur; Pyc., pycnocline.

1.5 L’écosystème marin arctique

1.5.1 Configurations géographique et océanographique

Approximativement centré sur le pôle nord, l’Océan Arctique forme une méditerranée délimitée par les masses continentales européenne, asiatique, américaine, l’immense ile du Groenland, et par le vaste archipel arctique canadien (Figure 1.2). Ce système océanique comprend en son milieu les bassins Amérasien et Eurasien, de 3000 à 5000 m de profondeur, entourés de vastes plateaux continentaux parfois très peu profonds qui occupent plus de 50% de la surface océanique (Jakobsson 2002). Avec une superficie estimée à 14 056 000 km^2, l’Océan Arctique est de loin le plus petit et le moins profond des cinq océans de notre planète. Les échanges entre la méditerranée arctique et les Océans Atlantique et Pacifique se faisant principalement par les détroits étroits de Fram et de Béring, respectivement, les bassins et la majorité des mers arctiques se retrouvent fortement influencés par l’afflux de masses d’eau de faible salinité venant du Pacifique et le débit des grands fleuves sibériens (Ob, Ienisseï et Lena), et du fleuve Mackenzie du côté américain (Yamamoto-Kawai et al. 2008; Yamamoto-Kawai et al. 2009b). Ces apports d’eau de salinité nulle à réduite, combinés à la faible évaporation liée aux températures froides de l’eau et de l’atmosphère en surface, font de l’Océan Arctique un gigantesque réservoir d’eau relativement douce (comparativement aux eaux de l’Atlantique) qui détient un rôle non négligeable dans la dynamique climatique globale et dans les processus de convection profonde alimentant la circulation océanique dans le nord-Atlantique (Broecker 1991). Cette couche moins salée en surface est notamment responsable de la forte stratification haline caractéristique de l’Arctique central et certaines de ses mers périphériques du bord américain (Carmack 2007). Une stratification aussi prononcée affecte la capacité des processus physiques (upwelling, convection) à assurer le mélange entre la partie supérieure de la colonne d’eau et la couche sous-jacente de l’halocline traditionnellement plus riche en sels nutritifs (nitrates, silicates) (Carmack et al. 2004; Tremblay et al. 2008). Ce contrôle du renouvèlement des nutriments dans la zone euphotique exerce à son tour une contrainte sur la production primaire pélagique à la base de la plupart des réseaux trophiques pélagiques et benthiques arctiques (Li et al. 2009; Tremblay et al. 2012b).

D’un autre côté, c’est cette même mince couche de mélange dessalée flottant à la surface de l’Océan Arctique qui a permis, sous l’effet des températures atmosphériques polaires négatives, la formation d’une banquise permanente dont l’existence remonterait à 2-3 millions d’années, voire 13 à 15 millions d’années, avec toutefois des hiatus possibles au cours des périodes interglaciaires (Polyak et al. 2010). Ce couvert de glace pérenne, encore appelé pack central, est certainement l'élément le plus emblématique du milieu marin arctique. La superficie minimale du couvert de



1, Plateau continental du Mackenzie; 2, Golfe d'Amundsen; 3, Baie de Franklin;
4, Polynie des Eaux du Nord (NOW); 5, POlynie des Eaux du Nord-Est (NEW)

Figure 1.2. Bathymétrie de l'Océan Arctique et de ses mers périphériques.

glace, qui est en moyenne de $6,14.10^6$ km^2 sur la période 1979-2010 (NSIDC 2012), est atteinte à la fin de la saison de fonte en septembre. Au retour de la longue saison froide, l'étendue englacée croît rapidement par accrétion de glace nouvelle, d'une part sur le pack central mobile localisé au dessus des bassins profonds, et d'autre part par la formation de la banquise saisonnière rattachée à la côte qui progresse vers le nord. Les bassins, la plupart des mers périphériques arctiques, ainsi que des zones adjacentes du Pacifique et de l'ouest de l'Atlantique, se retrouvent recouverts d'une chape de glace marine qui atteint son expansion et son épaisseur maximales en mars ($15,6\ 10^6$ km^2) (Comiso 2006), avant que le cycle saisonnier de fonte ne s'enclenche lentement. La glace et l'épaisseur variable de neige la recouvrant, affectent considérablement les transferts d'énergie et de matière entre l'atmosphère et l'océan sous-jacent en servant d'isolant à l'interface entre les deux (Iacozza et Barber 1999). Par exemple, la banquise, qui peut persister jusqu'à 10 mois dans des régions telles que le centre de l'archipel arctique canadien (Conover et Huntley 1991), ne permet qu'à une infime partie des radiations photosynthétiquement actives de pénétrer la couche de surface sous la glace et réduit la production primaire pélagique à une courte saison de quelques mois sur un cycle annuel. Toutefois, à la frontière entre la banquise de terre et le pack central qualifiée de système de chenaux de séparation circumarctique, se forment des polynies récurrentes connaissant des conditions de glace moins sévères que les zones adjacentes en raison de processus physiques complexes bien localisés (Barber et Massom 2007). Un tel exemple est la polynie du Cap Bathurst qui s'ouvre dans l'est du golfe d'Amundsen aux confins sud-est de la mer de Beaufort (Tremblay et al. 2012a). Dans ces polynies, le retrait de la couverture de glace plus tôt au printemps entraine un prolongement de la période d'insolation intense qui rallonge à son tour la saison de production primaire. Cela en fait généralement des sites de productivité biologique accrue quand cette augmentation de l'insolation est accompagnée d'un enrichissement des eaux de surface en sels nutritifs nouveaux (Tremblay et al. 2006; Ardyna et al. 2011; Forest et al. 2011b).

Le cycle saisonnier fortement contrasté d'éclairement solaire est une autre des grandes spécificités des hautes latitudes arctiques. En faisant alterner des périodes plus ou moins longues (en fonction de la latitude) de nuit polaire et de soleil de minuit, ce régime de lumière est en majeure partie responsable de la haute saisonnalité de la production primaire à la base de la banquise et dans la zone euphotique (Horner et Schrader 1982b). Les changements de luminosité influencent également les comportements de migration du zooplancton et des poissons (Varpe et Fiksen 2010).

1.5.2 Réseaux trophiques pélagiques arctiques

Au cours des derniers millions d'années, les conditions climatiques extrêmes propres à l'Océan Arctique ont façonné des écosystèmes marins uniques caractérisés par des organismes adaptés aux températures glaciales, à l'alternance entre la nuit polaire et le soleil de minuit, une banquise saisonnière ou permanente, des eaux de surface stratifiées et limitées en nutriments, ainsi qu'à un cycle de production primaire extrêmement saisonnier. L'ours polaire, l'éléphant de mer et le narval, à la survie liée à la banquise (Stirling 1997; Tynan et DeMaster 1997), sont sans doute les représentants les plus emblématiques de ces hyper-spécialistes endémiques des mers arctiques (Figure 1.1). Ces imposants carnivores, de même que les poissons et oiseaux marins, dépendent en premier lieu de la fixation photosynthétique de carbone et du transfert efficace de cette énergie entre les producteurs primaires et des composantes clés du zooplancton des réseaux trophiques arctiques. À ces réseaux il est aisé d'ajouter une dimension humaine en incluant par exemple les communautés inuit de l'Amérique du nord et du Groenland dont une grande part de l'apport en protéines, acides gras oméga-3, et autres composés nutritionnels garants de bonne santé, est assurée par la chasse des vertébrés occupant les niveaux trophiques supérieurs (Hovelsrud et al. 2008; Zeller et al. 2011).

Dans les eaux arctiques qui connaissent une couverture de glace saisonnière, la production primaire à la base du réseau trophique classique est assurée par les micro-algues de glace et du phytoplancton (Horner et Schrader 1982a). La saison de production primaire débute quand l'atteinte d'un niveau d'irradiance incidente critique (~2-9 μE m^{-2} s^{-1}) à l'interface glace-eau au printemps (Horner et Schrader 1982b; Gosselin et al. 1986) enclenche la croissance des cellules d'algue de glace adaptées à une faible luminosité (Ban et al. 2006). À mesure que les niveaux de radiation photosynthétiquement active augmentent sous la banquise, les algues de glace utilisent le stock de sels nutritifs rechargé pendant l'automne et l'hiver pour former une efflorescence qui culminera avant la débâcle (Tremblay et al. 2012b). La reconstitution des stocks de macronutriments dépend en grande partie de l'érosion de l'halocline par des processus physiques tels que des vagues internes, fréquentes tempêtes automnales, et des phénomènes localisés d'upwelling et de convection (Tremblay et al. 2008). Après la phase d'efflorescence, les cellules d'algue de glace allouent une quantité croissante de carbone à la biosynthèse de lipides (Lee et al. 2008), en plus de relâcher de grandes quantités de carbone organique dissous et de particules d'exopolymères transparents (Riedel et al. 2008). À la fonte de la glace, des amas d'algues de glace riches en lipides sont ainsi libérés dans la colonne d'eau où ils représentent une source de nourriture hautement énergétique pour le zooplancton et les micro-organismes planctoniques (Søreide et al. 2010; Leu et al. 2011). En dépit de leur contribution moindre à la production primaire marine, de l'ordre de 3 à 7% du total dans des mers périphériques arctiques (Gosselin et al. 1997; Forest et al. 2011b), les algues de glace pourraient être particulièrement importantes pour les communautés benthiques et la séquestration de carbone dans les sédiments (Hargrave et al. 2002; Carroll et Carroll 2003; Renaud et al. 2007). Une chute tôt en saison, quand le broutage n'est pas à son plein, et une vitesse élevée de sédimentation des amas d'algues de glace leur permettrait d'échapper en partie à l'interception et au recyclage dans la colonne d'eau (Michel et al. 1997; Michel et al. 2002).

La production d'algue de glace est rapidement suivie par celle du phytoplancton qui peut même débuter sous la glace quand suffisamment de lumière finit par atteindre les eaux de surface (Fortier et al. 2001; Mundy et al. 2009; Forest et al. 2011b). Le phytoplancton domine nettement la production primaire totale annuelle (Gosselin et al. 1997). L'intensité et la durée de la première efflorescence phytoplanctonique dépend de la disponibilité en sels nutritifs, dont les quantités ont déjà été réduites lors de la production antérieure des algues de glace (Tremblay et Gagnon 2009). Les eaux marines d'une portion importante de l'Arctique étant soumises à une forte stratification thermohaline (Carmack 2007), cette efflorescence pélagique se révèle de courte durée et est généralement remplacée par une période de relativement faible productivité, parfois ponctuée de pics de production. Ces derniers sont alimentés par des remontées épisodiques d'eaux profondes plus riches en nutriments inorganiques (Mundy et al. 2009; Tremblay et al. 2011). Une fois les eaux de surface appauvries en nutriments, il se forme un maximum de chlorophylle sous-jacente, au niveau de la nitracline, qui persiste jusqu'à la fin de la saison de production (Martin et al. 2010). Cette production phytoplanctonique profonde peut représenter au moins 50% de la production annuelle nouvelle dans la colonne d'eau (Tremblay et al. 2008; Popova et al. 2010). Les grandes cellules algales que sont les diatomées dominent les assemblages d'algues de glace et de phytoplancton en début de saison de production (Terrado et al. 2011), ainsi que les poussées épisodiques subséquentes de production générées par les phénomènes de remontée d'eau profondes. Lorsque les conditions de lumière et/ou de nutriments deviennent limitantes pour la production primaire, des flagellées et d'autres cellules de petite taille comme *Micromonas* sp. tendent à prendre le dessus de la communauté de protistes (Lovejoy et al. 2007).

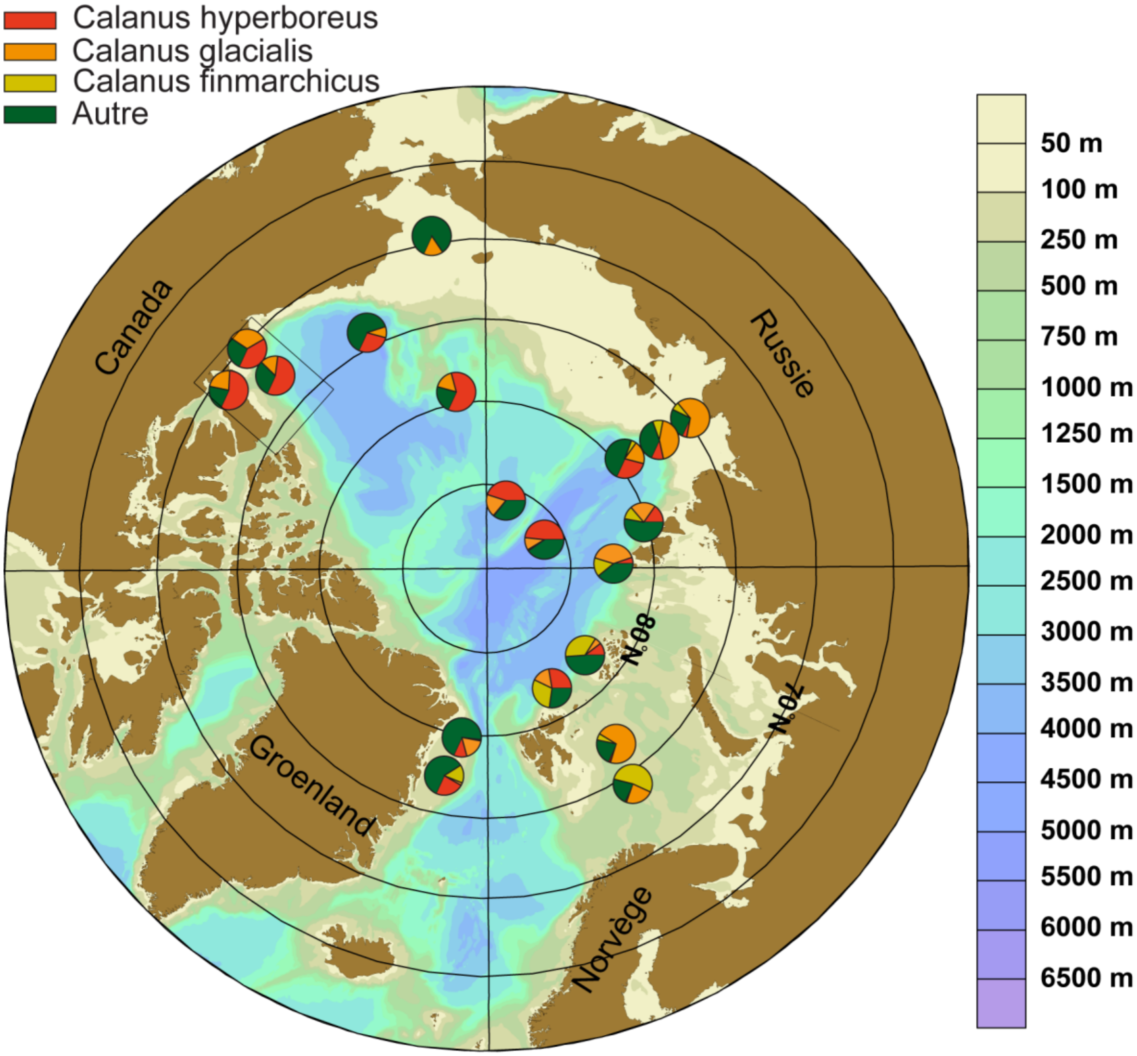
Les organismes métazoaires dominant le zooplancton arctique ont du développer des stratégies sophistiquées dans leur cycle biologique afin de tirer avantage de l'intense saisonnalité de la synthèse de matière organique dans le système épipélagique, et de cette dynamique particulière au sein des assemblages de producteurs primaires (Conover et Huntley 1991; Varpe 2012). Le zooplancton doit également survivre dans les eaux froides et sombres de mers englacées pendant la majorité de l'année. Les adaptations à ces conditions se manifestent notamment chez certains par des migrations verticales saisonnières, de longues périodes d'hivernage en repos métabolique (diapause), l'hyperspécialisation trophique comme chez l'espèce clé *Calanus hyperboreus*, ou au contraire un comportement d'alimentation opportuniste. Ces stratégies ont toutes des incidences importantes sur le fonctionnement de la pompe biologique, le zooplancton étant en mesure de détourner la majeure partie (66-79%) de la production primaire nouvelle (Tremblay et al. 2006; Forest et al. 2011b).

1.6 Le zooplancton arctique de la mer de Beaufort

1.6.1 Composition taxonomique et trophique

Les communautés de zooplancton sont moins diversifiées dans les mers des hautes latitudes que dans les régions subtropicales et tempérées (Woodd-Walker et al. 2002). Dans les bassins arctiques profonds, Kosobokova et al. (2011) ont relevé lors de leur important effort de recensement un total de 174 espèces zooplanctoniques, en comptant les espèces résidentes et expatriées des Océans Atlantique et Pacifique. La comptabilité d'Archambault et al. (2010) fait état d'une richesse de 372 espèces dans les eaux arctiques canadiennes, qui se compare bien avec celle des eaux nord-pacifiques du pays (381 espèces). En restreignant le territoire de recensement au sud-est de la mer de Beaufort, ce sont 49 taxons zooplanctoniques qui ont été énumérés à l'automne 2002 (Darnis et al. 2008).

Quelque soit leur richesse spécifique, les communautés de mésozooplancton (taille entre 0,2 et 20 mm) des régions océaniques arctiques (>200 m de profondeur) sont systématiquement dominées par la même combinaison de sept à huit taxons de copépodes, en comptant le copépode boréal *Calanus finmarchicus* dans les régions fortement influencées par l'Océan Atlantique (Ashjian et al. 1995; Thibault et al. 1999; Arashkevich et al. 2002; Auel et Hagen 2002; Ringuette et al. 2002; Ashjian et al. 2003; Darnis et al. 2008). En mer de Beaufort, les copépodes néritiques *Calanus glacialis*, *Pseudocalanus* sp., les plus océaniques *Calanus hyperboreus*, *Metridia longa*, *Triconia borealis*, *Microcalanus* sp., et l'espèce ubiquiste *Oithona similis* peuvent représenter, à eux seuls, 91 et 85% des abondance et biomasse totales respectives du mésozooplancton (Darnis et al. 2008; Forest et al. 2008). Avec près de 50% de la biomasse, le grand copépode *C. hyperboreus* prédomine nettement dans les zones les plus profondes (Figure 1.3), où les contributions des deux autres grands calanoïdes *C. glacialis* et *M. longa* sont également assez importantes (Forest et al. 2011a). La représentation des quatre autres bien plus petites espèces est forte essentiellement en terme d'abondance (Hopcroft et al. 2005).



Arashkevich et al. (2002); Ashjian et al. (1995; 2003); Darnis et al. (2008); Darnis et Fortier (2012); Hopcroft et al. (2010); Kosobokova et Hirche (2009); Kosobokova et Hopcroft (2010)

Figure 1.3. Contribution des trois copépodes calanidés *Calanus hyperboreus*, *C. glacialis* et *C. finmarchicus* à la biomasse du mésozooplancton de différentes régions de l'Océan Arctique.

L'intense broutage sur les efflorescences d'algues de glace et de phytoplancton est principalement le fait des herbivores *Calanus* sp., de l'omnivore *Metridia longa*, et dans une moindre mesure des copépodes de taille moyenne *Pseudocalanus* sp., qui sont distribués dans la couche de surface au printemps et une partie de l'été. Cela est avéré par la proportion élevée de pelotes fécales cylindriques de grands calanoïdes dans le flux fécal correspondant à la période d'intense production primaire (Forest et al. 2007). À ce titre, il faut mentionner la contribution non négligeable au flux de COP des grosses pelotes fécales de forme ellipsoïdale produites par les appendiculaires (Sampei et al. 2009a), zooplancton gélatineux fragile dont l'abondance est grandement sous-estimée dans les échantillons préservées de zooplancton. Un autre microphage, le ptéropode *Limacina helicina* est un autre consommateur parfois important de cellules algales sous la glace de la mer de Beaufort (Forbes et al. 1992).

Les trois petites espèces numériquement dominantes *Oithona similis*, *Triconia borealis*, et *Microcalanus* sp., fort probablement capables de se nourrir d'une grande variété de petites proies et particules organiques, sont considérées comme omnivores et détritivores. *Oithona similis* a une préférence pour les proies motiles et serait un prédateur efficace des dinoflagellés et ciliés appartenant au microzooplancton (Nakamura et Turner 1997; Castellani et al. 2005). Cet abondant copépode, aussi coprophage et consommateur de petites cellules algales (Hopkins et al. 1993; Atkinson 1996), participe à réduire le flux gravitationnel de COP (Gonzalez et Smetacek 1994). Les stratégies alimentaires de *T. borealis* et *Microcalanus* sp. sont très peu documentées. Sur la base de la composition en acides et alcools gras de *T. borealis*, et de sa structure mandibulaire se rapprochant de celle des autres Oncaeidés, on considère qu'il se nourrit de détritus adhérant à des agrégats en sédimentation, de pelotes fécales, et aussi que c'est un carnivore et semi-parasite capable de s'attaquer à des proies bien plus grosses que lui-même pour aspirer leurs fluides corporels (Darnis et al. 2012). La forme des mandibules de *Microcalanus* sp. suggère que c'est un consommateur de phyto-détritus et de petites proies animales (Michels et Schnack-Schiel 2005). Autre important omnivore zooplanctonique, *Metridia longa* a un régime alimentaire très varié (Haq 1967) auquel figurent en bonne place les œufs des autres copépodes (Sell et al. 2001).

Exprimée en terme de biomasse, la composante carnivore est une part non négligeable (12-21%) du mésozooplancton du golfe d'Amundsen et du talus continental de la mer de Beaufort (Darnis et al. 2008). Les carnivores les plus importants sont les chaetognathes, le copépode *Paraeuchaeta glacialis*, les amphipodes hypéridés, les cnidaires et cténophores.

1.6.2 Migrations verticales

À ce jour, seule l'étude de Benoit et al. (2010) sur la migration nycthémérale de la morue arctique dans le sud-est de la mer de Beaufort fait également mention de la fluctuation journalière de la distribution verticale de trois espèces de copépodes sous la banquise de la baie de Franklin en mars. Les migrations saisonnières des *Calanus,* qui dominent de beaucoup la biomasse zooplanctonique de la région, ne sont donc pas documentées.

Les recherches sur la variabilité saisonnière, ou même journalière, de la distribution verticale du zooplancton des régions arctiques exigent de lourds investissements pour la récolte et l'analyse des nombreux échantillons de zooplancton nécessaires à la réalisation d'une série exploitable de profils de distribution. En conséquence, rares sont les études décrivant les migrations saisonnières du zooplancton arctique à l'échelle d'un cycle annuel. Quelques campagnes d'échantillonnage de longue durée, menées à partir de stations de glace dérivantes dans les bassins arctiques (Johnson 1963; Dawson 1978; Vinogradov 1997), ou à leur périphérie (Ashjian et al. 2003), ont bien permis d'établir des séries temporelles utiles à décrire les patrons de distribution saisonniers d'espèces importantes. Toutefois, l'interprétation poussée de l'information ainsi produite sur la dynamique de la distribution verticale est rendue difficile par le fait que plusieurs régions hydrographiques, avec possiblement des populations distinctes d'organismes zooplanctoniques, ont été échantillonnées durant ces longues dérives. C'est le cas pour la station de glace SHEBA qui, entre octobre 1997 et octobre 1998, a dérivé à travers quatre régions de l'Arctique de l'ouest aux caractéristiques hydrographiques bien différenciées (Ashjian et al. 2003). Ces quelques études, et celle de Hirche (1997) en mer du Groenland, ont cependant permis de mettre en évidence une grande variabilité spatiale dans la profondeur d'hivernage de *Calanus hyperboreus*, l'espèce qui semble réaliser les migrations saisonnières les plus extensives (Figure 1.4). Un autre enseignement est que, parmi les taxons dominants, les migrations de grande amplitude existent surtout chez le zooplancton de grande taille. Mais, *Metridia longa* ferait essentiellement de migrations nycthémérales (Vinogradov 1997; Ashjian et al. 2003; Daase et al. 2008). Dans les mers d'Irminger et du Groenland, seule une portion de la population de *Oithona* spp. effectue une migration verticale saisonnière de faible ampleur, mais pas *Triconia* (*Oncaea*) spp. (Richter 1994; Gislason 2003).

Le cas des migrations nycthémérales dans les eaux arctiques est mieux documenté que celui des migrations saisonnières. Il est admis que c'est le changement relatif de l'intensité lumineuse à des moments d'un cycle nycthéméral qui déclenche les migrations ascendantes et descendantes des organismes (Fortier et al. 2001; Berge et al. 2009; Benoit et al. 2010). En raison de la forte saisonnalité du régime de lumière aux hautes latitudes, on devrait donc s'attendre à des migrations

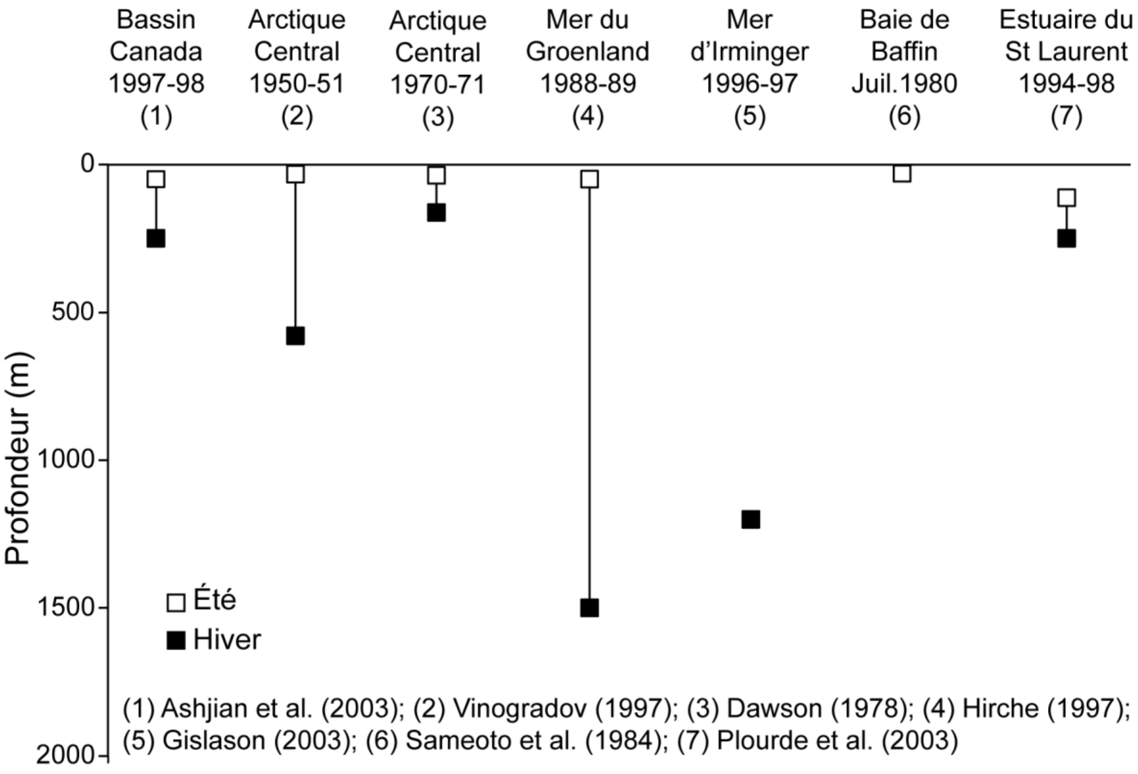


Figure 1.4. Distributions verticales estivales et hivernales des femelles adultes du copépode Calanus hyperboreus à différents sites de l'Arctique et de l'Atlantique Nord.

nycthémérales soutenues pendant les équinoxes de printemps et d'automne, et à une réduction, voire une absence, de la migration au fort de l'hiver et de l'été quand les changements d'irradiance sont moindres. À ce sujet, des conclusions divergentes ressortent des différentes études sur ce type de migration. L'analyse de données acoustiques obtenues par la technique Doppler, employée sur des mouillages océanographiques dans les fjords du Svalbard, a mis en évidence des migrations pendant la nuit polaire et le soleil de minuit, bien que ces dernières soient dominées par des mouvements asynchrones (Cottier et al. 2006; Berge et al. 2009; Wallace et al. 2010). Malheureusement, cette approche ne permet pas l'identification des migrateurs. L'emploi de filets a pu montrer que *Pseudocalanus* sp., *Calanus glacialis* et *C. hyperboreus* font des migrations nycthémérales sous la banquise de la Baie d'Hudson et du détroit de Barrow pendant la période de jour permanent (Conover et al. 1986; Runge et Ingram 1991; Fortier et al. 2001). Par contre, les copépodes dominants ne semblent pas s'engager dans des mouvements verticaux sous le soleil de minuit en mer de Barents, dans la polynie des Eaux du Nord-Est, au nord de la baie de Baffin, ou encore dans l'est de l'Arctique canadien (Longhurst et al. 1984; Ashjian et al. 1995; Blachowiak-Samolyk et al. 2006). Le consensus ressortant des études de ce genre en Arctique et Antarctique est que les migrations verticales nycthémérales aux hautes latitudes, quand elles ont lieu, se font à une bien plus petite échelle (quelques mètres) que celles observées dans les régions tempérées et subtropicales (Vinogradov 1997; Tanimura et al. 2008).

1.6.3 Le complexe d'espèces *Calanus*

Dans l'Arctique au sens large, le complexe d'espèces *Calanus* peut compter jusqu'à quatre éléments : *C. glacialis* et *C. hyperboreus*, et les expatriés *C. finmarchicus* (de l'Atlantique) et *C. marshallae* (du Pacifique) (Ji et al. 2012). Toutefois, seules les deux premières espèces, endémiques à l'Arctique, disposent des adaptions essentielles à maintenir des populations viables (reproductrices) sous ces conditions environnementales extrêmes (Hirche et Kosobokova 2007). Par exemple, la reproduction de *C. hyperboreus* a lieu en profondeur pendant l'hiver où, en l'absence de nourriture, elle est alimentée par les abondantes réserves lipidiques des femelles (Hirche et Niehoff 1996). *Calanus glacialis* est également capable de pondre sans nourriture mais la majorité de sa production d'œufs sera alimentée d'abord par la consommation d'algues de glace, et ensuite de phytoplancton une fois lancée la saison de production primaire (Swalethorp et al. 2011). L'avantage de ces stratégies de reproduction précoce est de permettre à la progéniture de ces deux espèces arctiques, éclose en avance ou proche de la première efflorescence importante de phytoplancton, d'être prête à exploiter au mieux la courte mais intense saison estivale de production biologique (Conover et Huntley 1991).

Par une pression de broutage élevée sur la production primaire microalguale (diatomées et dinoflagellés), les grands copépodes *Calanus* sp. ont la capacité d'élaborer en l'espace de quelques semaines d'immenses réserves lipidiques, principalement sous la forme d'esters cireux, pouvant dépasser 60% de leur masse sèche à la fin de la saison d'alimentation (Falk-Petersen et al. 2009). L'espèce la plus grande, *C. hyperboreus*, est aussi la plus efficace à accumuler des lipides essentiels (Pasternak et al. 2001) et à biosynthétiser des composés lipidiques aux chaines les plus longues, et donc avec un contenu en énergie supérieur (Albers et al. 1996). Dans ces réserves lipidiques, des marqueurs de dinoflagellés comme l'acide docosahexaénoïque (DHA), un acide gras polyinsaturé oméga-3, sont des constituants essentiels des lipides polaires dans les membranes cellulaires de tous les animaux où ils assurent fluidité, compressibilité et perméabilité (Falk-Petersen et al. 2009). Par une domination franche de la biomasse zooplanctonique et la concentration de grandes quantités de lipides, les *Calanus* arctiques constituent les herbivores principaux et un maillon crucial du transfert efficace d'énergie et de lipides structuraux essentiels des producteurs primaires de la zone euphotique vers les poissons, oiseaux marins et baleines zooplanctivores (Figure 1.1).

De plus, les stades de développement avancés de ces deux espèces entreprennent des migrations saisonnières à plusieurs centaines de mètres de profondeur où ils hivernent en état de repos métabolique parfois pendant 10 mois de l'année (Hirche 1997; Ashjian et al. 2003). La perte en profondeur, par respiration et mortalité, de ce carbone préalablement mis en réserve à la surface devrait faire de *C. hyperboreus* et *C. glacialis* des contributeurs significatifs à l'exportation de carbone vers l'intérieur de l'Océan Arctique.

1.7 L'écosystème marin arctique face aux effets du réchauffement climatique

La zone arctique subit plus intensément les contrecoups des changements climatiques que les autres régions du globe (Serreze et Barry 2011). Les températures de surface de cette région augmentent de deux à quatre fois plus vite que la moyenne globale, un phénomène communément qualifié d'amplification arctique. Une suite complexe de causes, opérant à différentes échelles temporelles et spatiales, sont mises de l'avant pour expliquer l'amplification arctique (Screen et al. 2012). Cela inclut entre autres les changements de concentration de glace de mer, de transport atmosphérique et océanique de chaleur, de couverture nuageuse et de vapeur d'eau (Serreze et Barry 2011).

La manifestation la plus spectaculaire des phénomènes liés au réchauffement climatique est le déclin drastique de la banquise permanente. Les données satellitaires depuis 1979 démontrent que la couverture de glace permanente arctique disparait plus rapidement sur le terrain que dans les simulations des modèles climatiques utilisés dans le dernier rapport du GIEC (Groupe d'Experts Intergouvernemental sur l'Évolution du Climat) (Stroeve et al. 2012a). L'étendue minimale de glace de mer, traditionnellement atteinte à la fin de la saison de fonte en septembre, a battu un nouveau record (3,41 10^6 km^2) qui pulvérise le précédent de 2007 de 18% (NSIDC 2012). Au cours des dernières décennies, la tendance à la baisse de l'étendue minimale de glace n'a cessé de s'accentuer, passant de -9% par décennie pendant la période 1979-2000 (Comiso 2002) à -12,9% quand les données satellitaires sont prolongées jusqu'à 2011 (Stroeve et al. 2012b). De plus, l'Océan Arctique perd sa glace pluriannuelle à un rythme soutenu, -42% entre 2005 et 2008 (Polyakov et al. 2012). Jadis dominante, elle est maintenant largement remplacée par une couche de glace saisonnière de première année plus fine (Maslanik et al. 2007). Une conséquence directe en est que l'épaisseur moyenne de la banquise hivernale a été réduite de 50% par rapport au valeurs estimées en 1980 (Kwok et Rothrock 2009). Exploitant les dernières données d'étendue et d'épaisseur de glace marine dans des modèles actualisés, Wang et Overland (Wang et Overland 2012) prédisent que la région arctique en entier deviendra libre de glace au cours d'un été dans les années 2030.

Ces changements drastiques dans le régime des glaces et, à terme, la disparition de la banquise auront des répercussions considérables sur l'écosystème marin arctique et les processus qui lui sont associées, dont les cycles biogéochimiques d'éléments comme l'azote et le carbone (Doney et al. 2012). Au niveau des facteurs biotiques, des déplacements d'aires de distribution d'espèces ; des altérations de la croissance, des conditions physiologiques, comportementales et phénologiques, ainsi que et des bouleversements à l'échelle des communautés et des régimes de production biologique seront parmi les plus importants à suivre (Wassmann et al. 2011). Toutefois, prédire les réponses des composantes de l'écosystème aux changements biotiques et abiotiques s'annonce une tâche des plus ardue.

Déjà, par leur interprétation d'une série temporelle de données satellitaires de couleur de la surface de l'eau, Arrigo et van Dijken (2011) indiquent une augmentation de 20% de la production primaire nette totale annuelle du phytoplancton de l'Océan Arctique et de ses mers périphériques. Cet accroissement serait largement induit par l'allongement de la saison de croissance (+ 45 jours) provoqué par le recul de la période d'englacement dans certaines mers périphériques. Par contre, la diminution importante de la couverture de glace au dessus des plateaux de l'Arctique Pacifique et du Bassin Canada au cours des dernières années n'a pas été suivie par une augmentation de la biomasse algale totale (Li et al. 2009; Grebmeier et al. 2010). L'intensification de la stratification qui a accompagné le recul de la glace en été a pour effet de restreindre la remontée de sels nutritifs dans la zone euphotique (McLaughlin et Carmack 2010). Ces conditions de limitation en nutriments favorisent les petites cellules du picophytoplancton, comme *Micromonas* sp., qui se sont substituées aux cellules plus grosses dans le Bassin Canada (Li et al. 2009). Par un effet de cascade trophique, ces réductions de taille de cellules dans les assemblages de producteurs primaires pélagiques avantageront probablement le microzooplancton, plus aptes à filtrer les petites cellules (<2 µm) que ne le sont les grands copépodes *Calanus* sp. La mise en place de tels systèmes épipélagiques augmentera sans nul doute le recyclage du CO_2 en surface et, donc, affectera négativement la pompe biologique de carbone. L'augmentation de production primaire pélagique se limitera très certainement à des zones des plateaux continentaux où la combinaison de la disparition de la glace avec des vents favorables stimulera des épisodes plus fréquents de remontée d'eau profondes enrichies en sels nutritifs (Tremblay et al. 2012b). Dans certaines régions arctiques et subarctiques soumises à une couvert de glace saisonnier, les blooms de phytoplancton ont lieu plus tôt que dans le passé (Kahru et al. 2011). Avec la réduction de la banquise, la saison de production des algues de glace devrait donc en toute logique se contracter, affectant certains organismes du zooplancton qui bénéficient de cette production hâtive de matière organique de haute qualité nutritive pour avancer leur saison de reproduction (Leu et al. 2011).

Les communautés de zooplancton seront affectées d'abord par les bouleversements dans la production des algues de glace et du phytoplancton à la base du réseau trophique. Il a été proposé que la réduction de la période englacée se fera à l'avantage des populations des grands copépodes calanoïdes et *Pseudocalanus* sp. qui profiteront de périodes de croissance et d'alimentation plus longues, et de températures ambiantes plus élevées stimulant le développement des juvéniles en surface (Ringuette et al. 2002; Darnis et al. 2008). Cependant, des risques de décalage entre des lancements de plus en plus précoces de la production primaire, qui influencent le moment des pics de production, et des étapes cruciales pour le recrutement des copépodes herbivores dominants sont aussi avancés (Soreide et al. 2010; Leu et al. 2011). Parmi les multiples autres menaces qui pèseront sur le zooplancton arctique, on peut souligner encore une fois la réduction de taille de cellules dans les assemblages d'algues pélagiques prévue avec l'intensification de la stratification (Li et al. 2009; Moran et al. 2010).

En outre, une circulation océanique de surface intensifiée par la diminution de la superficie de glace de mer, de même que l'amplification de l'influx d'eau intermédiaire d'origine atlantique (Polyakov et al. 2011), provoqueront des entrées encore plus massives d'espèces boréales d'origine pacifique et atlantique (Hopcroft et al. 2010). Avec la relaxation future des conditions environnementales, en particulier l'augmentation de la température ambiante, il y a le risque que des espèces invasives généralistes établissent des populations viables, exerçant alors une pression de compétition pouvant aboutir au déplacement d'espèces arctiques clés plus spécialisées. Les flux biogéochimiques sous la médiation de ces dernières en seraient certainement affectés. De tels signes de perturbation dans la composition des communautés zooplanctoniques n'ont pas encore été perçus dans l'Arctique Central lors de la comparaison de données contemporaines avec des données historiques datant de 50 ans (Kosobokova et Hopcroft 2010). Il reste que ce sont les mers en périphérie qui devraient être touchées en premier par ces bouleversements au sein du zooplancton. Grâce à des efforts d'échantillonnage soutenus, notamment dans le sud-est de la mer de Beaufort et en mer de Barents, des séries temporelles suffisamment longues sont en train de se construire pour permettre un suivi de ces changements.

Associée à la perte de glace de mer, l'augmentation de l'absorption de CO_2 par les eaux de surface cause leur acidification, un phénomène qui a notamment rendu la zone euphotique d'une partie du Bassin Canada sous-saturé pour le carbonate de calcium de type aragonite (Yamamoto-Kawai et al. 2009a). Ce sont là des conditions déjà défavorables pour les organismes comme les mollusques ptéropodes, un groupe parfois important du zooplancton arctique, qui forment de l'aragonite pour construire leur coquille calcaire. L'accroissement de l'acidification devrait nuire non seulement aux organismes calcificateurs du plancton mais aussi à tous les organismes en affectant divers processus physiologiques tels que la capacité de transport en oxygène (Fabry et al. 2008). L'augmentation de la température des eaux de surface (Steele et al. 2008) pourra également influencer les processus physiologiques et des organismes arctiques sténothermes devront possiblement modifier leurs comportement migratoire pour éviter des températures qui leur sont délétères.

1.8 Objectifs de recherche

La présente thèse, composée de trois articles de recherche (chapitres 2 à 4), s'applique à examiner les rôles des migrations verticales, des interactions trophiques et de la respiration de taxons dominants du mésozooplancton arctique dans le fonctionnement de la pompe biologique de CO_2. L'ensemble des analyses s'appuie sur des profils de zooplancton faits à haute résolution temporelle entre le 15 octobre 2007 et le 30 juillet 2008 dans le cadre du programme scientifique canadien Circumpolar Flaw Lead System Study (CFL) mené dans le sud-est de la mer de Beaufort.

Le premier chapitre a pour objectif principal de décrire les patrons de distribution verticale de sept espèces de copépodes qui dominent, en terme de d'abondance et/ou de biomasse, le zooplancton de la majorité des régions arctiques englacées toute ou partie de l'année. Ce chapitre comporte deux volets : (1) identifier les espèces dominantes impliquées dans des migrations verticales d'amplitude suffisante pour contribuer significativement au transport actif et au stockage de carbone en profondeur, et (2) examiner les relations qu'entretiennent la distribution verticale de ces copépodes et le déclenchement éventuel de comportements de migration avec les gradients verticaux de température, le couvert de glace et la disponibilité des ressources alimentaires.

Le deuxième chapitre examine plus spécifiquement le cycle vital du grand copépode herbivore *C. hyperboreus*, une espèce arctique dont la dominance de la biomasse zooplanctonique et les migrations saisonnières extensives désignent déjà comme un acteur potentiel important du transport actif respiratoire de carbone en profondeur. Notamment, une description détaillée est faite de son cycle de reproduction et de la dynamique de sa population. Ce travail tire profit du particulièrement faible englacement de 2007-2008 dans le sud-est de la mer de Beaufort pour tester l'hypothèse selon laquelle l'allongement de la saison libre de glace sur les plateaux continentaux stimulera la croissance de la population des grands copépodes herbivores.

Le dernier chapitre examine les migrations verticales de deux fractions de taille du zooplancton, 200-1000 µm et >1000 µm, et mesure leur respiration à différents niveaux de la colonne d'eau. L'objectif est de quantifier le recyclage du carbone sous la médiation du mésozooplancton ainsi que le flux actif respiratoire de carbone qui résulte de la migration en profondeur de certaines de ses composantes. Le rôle de ce transport actif sera comparé au flux gravitationnel de carbone particulaire estimé à l'aide de pièges à particules.

L'ensemble de ces objectifs servira à tester l'hypothèse simple selon laquelle le zooplancton des mers périphériques arctiques, dominé par de grands migrateurs saisonniers herbivores, joue un rôle déterminant dans le cycle biogéochimique du carbone en stimulant la pompe biologique par un transport actif de carbone de grande ampleur.

2. Chapitre 2 – Food, temperature and the seasonal vertical migration of key copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean)

2.1. Résumé

Nous avons examiné la migration verticale saisonnière (MVS) des stades copépodite de 7 copépodes arctiques dominants d'octobre 2007 à juillet 2008 dans le golfe d'Amundsen. Le grand herbivore pélagique *Calanus hyperboreus* s'est maintenu dans la couche Atlantique profonde de décembre à mi-avril, a rapidement envahi la couche de surface au début de l'efflorescence phytoplanctonique en début mai, et a débuté sa descente vers la profondeur d'hivernage en juillet. *C. glacialis* a hiverné à des profondeurs inférieures à *C. hyperboreus*, est monté dans la couche de surface en début avril au moment de l'efflorescence d'algue de glace, et est demeuré dans le maximum de chlorophylle sous-jacente (MCS) jusqu'à fin juillet. Le petit omnivore *Oithona similis* a lentement afflué vers la Couche Polaire de Mélange de février à avril, certains des animaux atteignant l'interface glace-eau en début avril à la première apparition des algues de glace. Le minuscule *Triconia borealis*, associé avec *C. hyperboreus* dans la couche Atlantique d'octobre à avril, a effectué une brève ascension en mai et est revenu en profondeur en juin. Les omnivores mésopélagiques *Metridia longa* et *Microcalanus pygmaeus* n'ont pas montré de MVS, mais des migrations ontogénétiques claires qui ont partitionné la colonne d'eau entre les différents stades copépodite. Les deux espèces ont pu être caractérisées d'intercepteurs aux profondeurs intermédiaires, s'alimentant du flux ascendant d'œufs de *C. hyperboreus* à la fin de l'hiver et au début du printemps, et sur la pluie de microalgues pendant le printemps-été. Dans une sorte de MVS inverse, le genre épipélagique *Pseudocalanus* spp. s'est distribué selon une étroite bande centrée à approximativement 50 m d'octobre à avril, ensuite est descendu sous la MCS de mai à juillet. Les copépodes ont généralement évité la lentille d'eau de surface chaude (2-8^{o}C) en été, mais ont facilement migré à travers le gradient (-1,7 ^{o}C à +0,3^{o}C) de la Couche Polaire de Mélange et l'Halocline Pacifique jusqu'à la couche Atlantique. La température a eu peu d'effet sur les déplacements verticaux des copépodes arctiques. Cependant, les différents patrons de migrations saisonnières et ontogénétiques ont dicté les régimes de température très différents vécus au cours d'un cycle annuel par chaque espèce et stade copépodite.

2.2. Abstract

We investigated the seasonal vertical migration (SVM) of the copepodite stages of 7 dominant arctic copepods from October 2007 to July 2008 in the Amundsen Gulf. The large pelagic herbivore *Calanus hyperboreus* resided in the deep Atlantic layer from December to mid April, rapidly invaded the surface layer at the onset of the phytoplankton bloom in early May, and started its descent to overwintering depth in July. *C. glacialis* overwintered at shallower depths than *C. hyperboreus*, moved into the surface layer in early April as ice algae bloomed, and remained in the sub-surface chlorophyll maximum (SCM) until late July. The small omnivore *Oithona similis* slowly rose into the Polar Mixed Layer from February to April, some animals reaching the ice-water interface in early April as ice algae first appeared. The minuscule *Triconia borealis* associated with *C. hyperboreus* in the Atlantic Layer from October to April, moved briefly upward in May and returned at depth in June. The mesopelagic omnivores *Metridia longa* and *Microcalanus pygmaeus* showed no SVM, but clear ontogenetic migrations that partitioned the water column among the different copepodite stages. The two species could be characterized as mid-depth interceptors, feeding on the upward flux of *C. hyperboreus* eggs in late winter-early spring and on the rain of microalgae in spring-summer. In a kind of reverse SVM, the epipelagic genus *Pseudocalanus* spp. distributed in a narrow band centered around 50 m from October to April, then descending under the SCM from May to July. Copepods generally avoided the lens of warm (2-8ºC) surface water in summer, but readily migrated across the (-1.7ºC to +0.3ºC) gradient from the Polar Mixed Layer and Pacific Halocline to the Atlantic Layer. Temperature had little effect on the vertical displacements of arctic copepods. But the different patterns of seasonal and ontogenetic migrations dictated the widely different temperature regimes experienced over the annual cycle by each species and copepodite stage.

2.3. Introduction

The low-diversity zooplankton of Arctic seas is dominated by the same guild of several copepod species (Longhurst et al. 1984; Kosobokova et al. 1998; Auel et Hagen 2002; Ringuette et al. 2002; Ashjian et al. 2003; Darnis et al. 2008). The large endemic calanoids *Calanus glacialis*, *C. hyperboreus* and the medium-size *Metridia longa* usually account for 50-90% of the biomass, whereas the small *Oithona similis*, *Triconia borealis* (formerly *Oncaea borealis*), *Pseudocalanus* spp., and *Microcalanus pygmaeus* prevail numerically. The herbivorous *Calanus* species are a staple for baleen whales (Harwood et Smith 2002), seabirds (Karnovsky et Hunt 2002), and the Arctic cod (*Boreogadus saida*), the dominant forage fish in arctic waters, which also feeds on *M. longa* and *Pseudocalanus* spp. (Michaud et al. 1996; Benoit et al. 2010). Smaller species of copepods form a trophic link between the microbial food web and larger zooplankton and fish larvae (Madsen et al. 2008). Thus, the ubiquitous copepods play a pivotal role in the energy transfer from primary producers to vertebrate predators at top levels in the arctic marine food web (Welch et al. 1992). Furthermore, diverse copepod activities such as grazing of ice algae and phytoplankton, the production of fast-sinking faecal pellets, coprophagy, carbon remineralisation by respiration, and vertical migrations have a deep influence on the biogeochemical carbon cycle in arctic marine ecosystems (Wassmann 1998; Darnis et Fortier 2012).

Arctic copepods have evolved different life strategies to maintain viable populations against the frigid temperatures and extreme light and sea-ice regimes that constrain ice-algal and phytoplankton production to the spring-summer season (e.g. Head et al. 1985; Conover et Huntley 1991; Hays et al. 2001; Gislason 2003). *Calanus* species graze efficiently on the diatom-dominated ice-algae and phytoplankton summer blooms at the surface (Tremblay et al. 2006; Forest et al. 2011b), and can build within a few weeks lipid reserves exceeding 60% of their dry mass to withstand fast during the following overwintering diapause of up to 10 months (Falk-Petersen et al. 2009). Each year, they perform vertical migrations of typically several hundred meters between the surface layer and overwintering depths (Dawson 1978; Hirche 1997; Ashjian et al. 2003). By contrast, *Metridia longa* and the small omnivores/detritivores *Oithona similis*, *Triconia borealis*, *Pseudocalanus* spp., and *Microcalanus pygmaeus* are believed to feed opportunistically, remain active year-round, and not to engage in extensive vertical migrations (Ashjian et al. 2003). As arctic copepods channel most of the energy from primary producers to higher trophic levels (e.g. Welch et al. 1992), their annual migration (or lack thereof) likely structures much of the pelagic ecosystem by dictating trophic interactions between the zooplankton and vertebrate predators (fish, mammals, and seabirds).

The winter vertical distributions of copepods in the thermally stratified Arctic Ocean and the impact of their annual vertical migration on the temperatures experienced by the different developmental stages are poorly documented. Yet, this information is crucial for the development of bioenergetic models that explore the potential response of key species to on-going and future shifts in the temperature, sea ice and primary production regimes of the ancillary seas of the Arctic Ocean (e.g. Ji et al. 2012; Maps et al. 2012; Thanassekos et Fortier 2012). During the International Polar Year, the multidisciplinary Circumpolar Flaw Lead System Study (Barber et al. 2010) provided an exceptional opportunity to monitor the offshore zooplankton community at a ca. biweekly sampling resolution from October 2007 to July 2008 in the Amundsen Gulf (Canadian Beaufort Sea). In the present study, we document the vertical migrations of the dominant copepods with emphasis on the average temperature experienced by the different copepodite stages (CI to adult) during their annual vertical migration in the thermally stratified Arctic Ocean. In particular, we address the expectation that, at the extreme cold temperatures prevailing in Artic seas (typically from -1.8 to 4ºC), all species seek the warmest temperatures available to maximize growth, maturation and reproduction.

2.4. Material and methods

2.4.1 Study area and oceanographic setting

The Amundsen Gulf is a large channel (~60000 km^2) connecting southeastern Beaufort Sea to the Canadian Arctic archipelago (Figure 2.1). Maximum depth of about 630 m occurs in a small central basin midway between the southern tip of Banks Island and shallow Darnley Bay. The water column in Amundsen Gulf comprises three layers: the nutrient-poor Polar-Mixed Layer ($S<31.6$; 0–50 m depth), the Pacific Halocline ($32.4<S<33.1$; 50–200 m), and the relatively warm Atlantic Waters ($S>34$; >200 m) (Carmack et Macdonald 2002).

Freeze-up begins in October at the coastal margins of Amundsen Gulf and ice consolidation over the entire region takes place in December with the connection of landfast ice to the perennial Beaufort Sea ice pack west of Banks Island (Galley et al. 2008). On average since 1979, sea ice starts to retreat in early June as the flaw lead polynya enlarges to form the Cape Bathurst Polynya complex (Barber et Hanesiak 2004). The extent and persistence of open water varies considerably from year to year (Arrigo et van Dijken 2004).

2.4.2 Sampling

The vertical distribution of zooplankton was determined at 78 stations in southeastern Beaufort Sea between 16 October 2007 and 30 July 2008 (Figure 2.1). Sixty-six stations were located in

Amundsen Gulf per se, 3 in Franklin Bay and 1 in shallow Darnley Bay. Thanks to record low ice concentration in the region in the winter 2007-2008 (Barber et al. 2010), 8 stations were sampled outside Amundsen Gulf, on the Mackenzie outer shelf, off the west coasts of Banks Island and as far north as McClure Strait, in October 2007 and spring-summer 2008. Sampling procedures are detailed elsewhere (Darnis et Fortier 2012). Briefly, a 0.50-m^2 aperture Hydrobios® multinet sampler carrying nine nets of 200-µm mesh size each fitted with a 2-L rigid codend was hauled vertically from 10 m above the bottom to the surface at a speed of 0.5 m s^{-1}. The nine nets were deployed sequentially. For each haul, three 20-m depth layers were sampled from 10 m above the seafloor upward and three 20-m depth layers sampled from 60 m depth to the surface. The remaining interval from 70 m above the bottom to 60 m from the surface was divided in three equal sampling layers, the thickness of which varied with station depth. Upon retrieval, the samples were subdivided in halves using a Motoda splitting box. One half from each codend was preserved in a borax-buffered seawater solution of 4% formaldehyde for taxonomic identification. The second half was used to assess zooplankton community biomass and respiration (Darnis et Fortier 2012).

Estimates of weekly ice coverage and profiles of temperature and *in situ* chlorophyll a (chl *a*) are from Darnis and Fortier (2012). The biomass of ice-algae are from Wold et al. (2011).

2.4.3 Zooplankton taxonomy and biomass

In the laboratory, the formalin-preserved zooplankton samples were rinsed, size fractionated on a 1000-µm sieve and re-suspended in distilled water. Successive known aliquots were taken from the 200-1000 µm fraction (Henson-Stempel pipette) and the >1000 µm fraction (Motoda splitting box), until approximately 300 animals from each fraction were counted, measured and identified to species or to the lowest possible taxonomic level under the microscope. The genus *Microcalanus* was attributed to *M. pygmeus*, but *M. pusillus* may have been present in the collections as well. Members of the genus *Pseudocalanus* (possibly a combination of *P. minutus*, *P. acuspes* and *P. newmani*, (Darnis et al. 2008)) were not identified to species because of uncertainties in distinguishing them. Carbon content for each taxon was calculated using published length-mass relationships for arctic zooplankton (Mumm 1991; Hopcroft et al. 2005; Forest et al. 2011a).

2.4.4 Vertical distribution

The weighted mean depth (WMD, m) and standard deviation ($Z_{s,}$ m) of the vertical distribution of phytoplankton (chl *a*) or zooplankton (carbon) biomass was calculated as:

$$WMD = \sum_{i=1}^{n} w_i d_i z_i \Big/ \sum_{i=1}^{n} d_i z_i \tag{1}$$

$$Z_S = \sqrt{\left(\sum_{i=1}^{n} w_i d_i z_i^2 \Big/ \sum_{i=1}^{n} d_i z_i\right) - WMD^2} \tag{2}$$

(Manly 1977; Dupont et Aksnes 2012), where w_i is the biomass per cubic meter within depth interval i, d_i is the thickness of depth interval i, and z_i is the midpoint depth of the interval.

2.5. Results

2.5.1 Sea-ice, temperature, and microalgal production

New and young ice started to form in late October in Amundsen Gulf (Figure 2.2a). The first-year ice cover reached >80% by late November and started to decline in early April. The ice algal bloom started in late March and peaked in late April and early May (Figure 2.2a). From November to early May, atmospheric cooling caused the progressive thickening of a surface layer of near-freezing temperature (<-1.6ºC) that extended down to 100 m by May (Figure 2.2b). Although remaining <0°C, temperatures progressively increased with depth from the Polar Mixed Layer to the base of the Pacific Halocline at ca. 200 m. Below that depth, 0 to 0.3ºC temperatures prevailed in the Atlantic Layer (Figure 2.2b). Starting in late May, the surface layer warmed up with temperature generally above 2ºC and reaching as high as 8ºC from the surface to 14 m on 21 July. Weak concentrations of phytoplankton (<1 µg L^{-1}) still persisted between the surface and 50 m at the start of sampling in October (Figure 2.2c). From early November to late April, phytoplankton biomass was undetectable throughout the water column. Phytoplankton production started in the cold surface layer in late April, intensified into a surface bloom in mid March, and evolved into a sub-surface maximum with algal biomass distributed under the lens of warm surface water (Figure 2.2c).

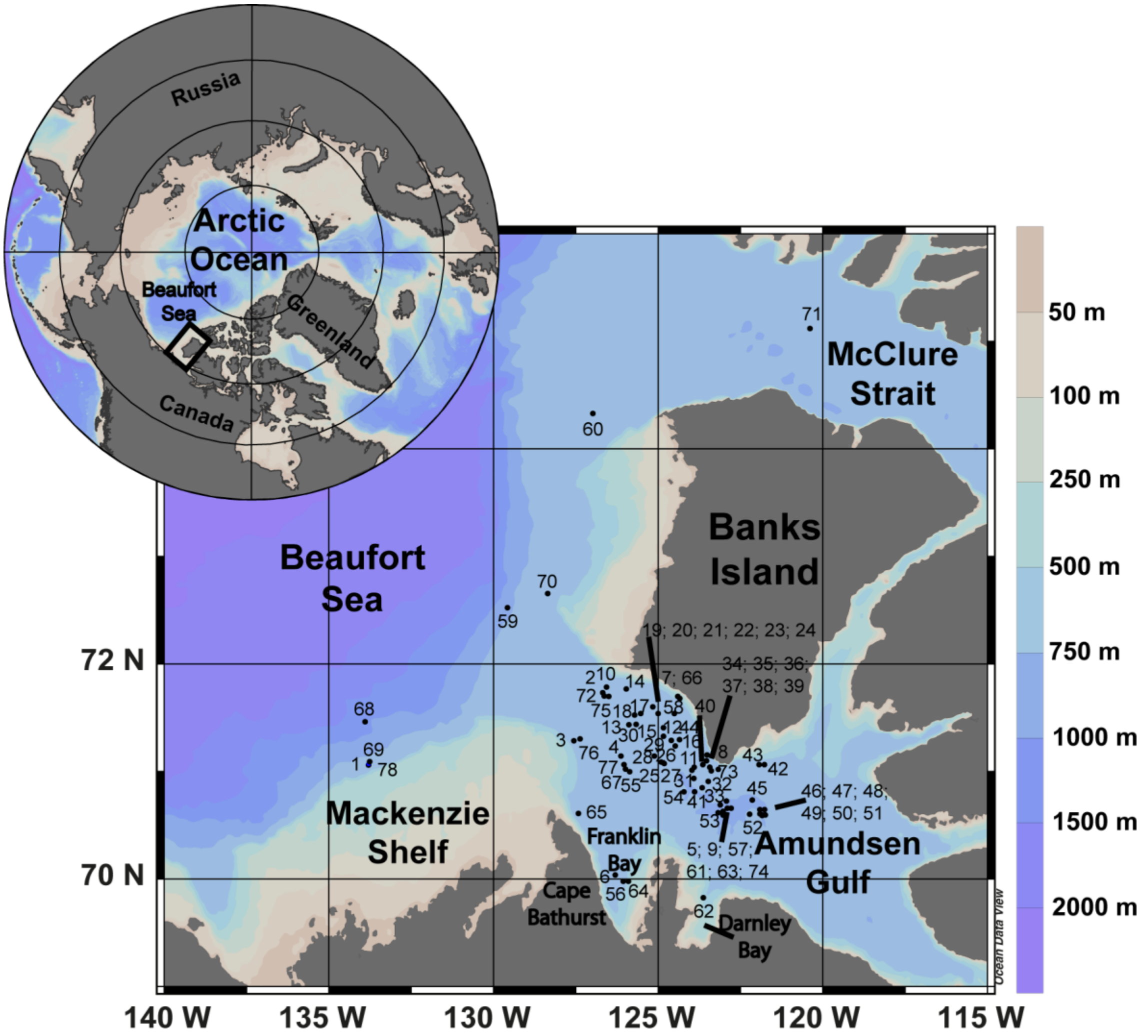


Figure 2.1. Bathymetry of the southeastern Beaufort Sea with the location of mesozooplankton sampling stations numbered in chronological order of sampling.

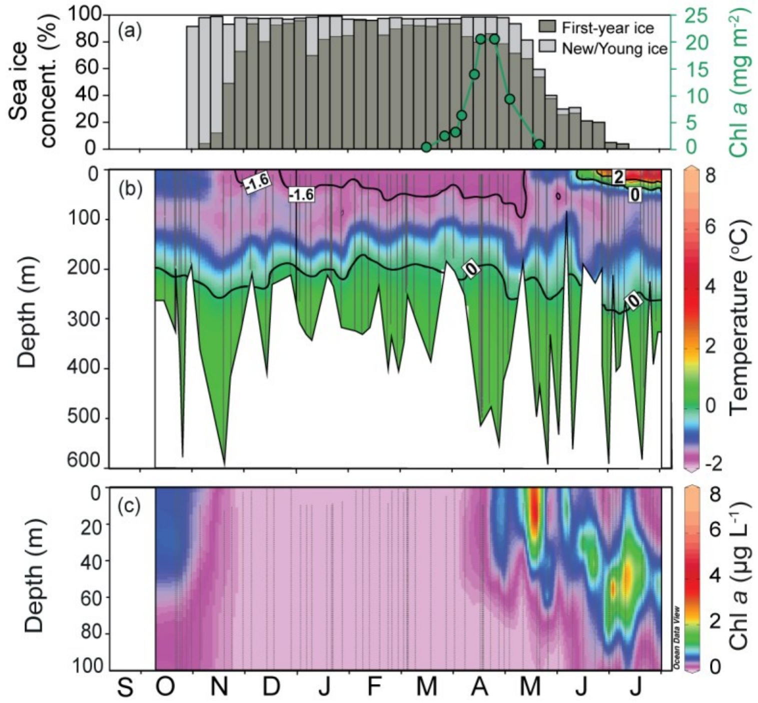


Figure 2.2. Time series of ice % concentration and ice-algae concentration in Amundsen Gulf (a) and corresponding time–depth sections of temperature from surface to bottom (b) and chl *a* concentration from the surface to 100 m (c) along the track of the ship from October 2007 to July 2008.

2.5.2 Time-depth sections of copepod biomass by species

Among copepod species, the seasonal vertical migration (SVM) of the overall population (pooled biomass of all copepodite stages) was most pronounced in the large calanoid *Calanus hyperboreus,* which remained primarily in the deep Atlantic Water (>200 m) from December to mid April, rapidly crossed the Pacific Halocline to invade the surface Polar Mixed Layer (PML, 0-50 m) at the onset of phytoplankton production in late April, and started its descent to overwintering depth in July (Figure 2.3a). *C. glacialis* winter depth distribution spanned the Pacific Halocline and the Atlantic Waters from 50 m to the bottom (Figure 2.3b). *C. glacialis* ascended into the Polar Mixed Layer in mid April and remained there until late July (Figure 2.3b). The small cyclopoid *Oithona similis* was distributed over both the Polar Mixed Layer (0-50 m) and the Pacific Halocline (50-200 m) from October to Mars, retiring to the Polar Mixed Layer from the end of March until July (Figure 2.3c). The small *Triconia borealis* congregated in the deep basins in November and December, progressively extended its distribution into the Pacific Halocline from January to May before starting its return at depth in June (Figure 2.3d). Few *T. borealis* ever entered the Polar Mixed Layer. The biomass of the medium-sized *Metridia longa* was low from October to late January as the population was made up primarily of the small CI-CIII. The species was distributed primarily in the cold Pacific Halocline with little evidence of SVM (Figure 2.3e). *Microcalanus pygmaeus* exhibited little SVM as well, distributing patchily over the Pacific Halocline and the deep Atlantic Layer throughout the year, with some entering the surface Polar Mixed Layer from April to June (Figure 2.3f). Except for some deepening of the population in June and July, the *Pseudocalanus* spp. complex presented no clear SVM, remaining in the Polar Mixed Layer and the shallower half of the Pacific Halocline throughout the year (Figure 2.3g).

2.5.3 Weighted mean depth of biomass by species (all stages pooled)

Calculation of the Weighted Mean Depth (WMD) and its standard deviation helped summarize the average vertical displacement of each species relative to the boundary between the Polar Mixed Layer and the Pacific Halocline (-1.6ºC isotherm) and between the Pacific Halocline and the Atlantic Layer (0ºC isotherm).

The weak phytoplankton biomass detected in October-November tended to sink with time towards the -1.6ºC isotherm at the boundary between the PML and the PH (Figure 2.4a). In June-July, the WMD of the subsurface chlorophyll maximum also coincided roughly with the -1.6ºC isotherm.

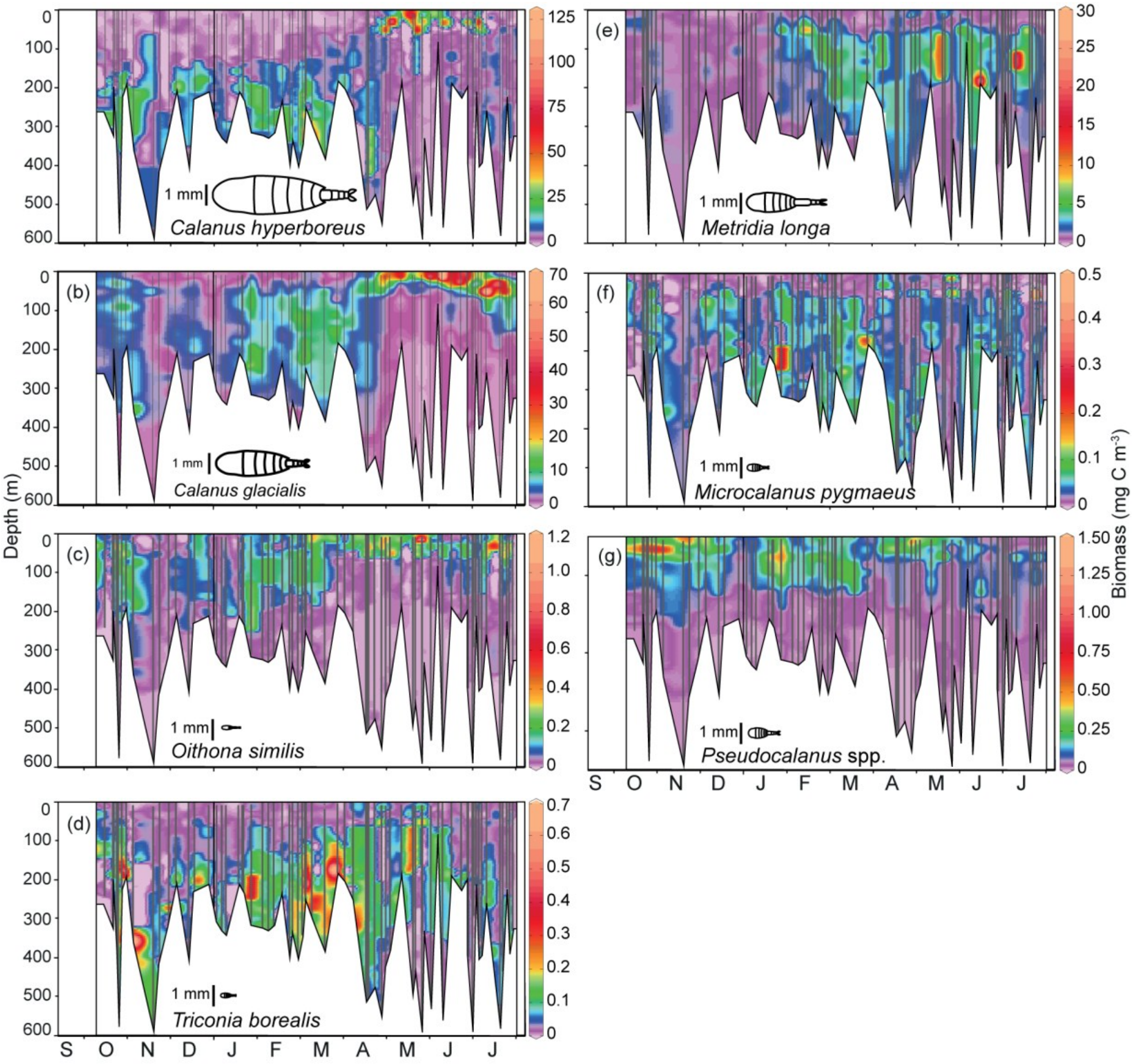


Figure 2.3. Time-depth sections of biomass of the seven dominant copepod species along the track of the ship in southeastern Beaufort Sea from October 2007 to July 2008. Vertical lines indicate sampling dates. All 78 stations (including 12 stations outside Amundsen Gulf) are included.

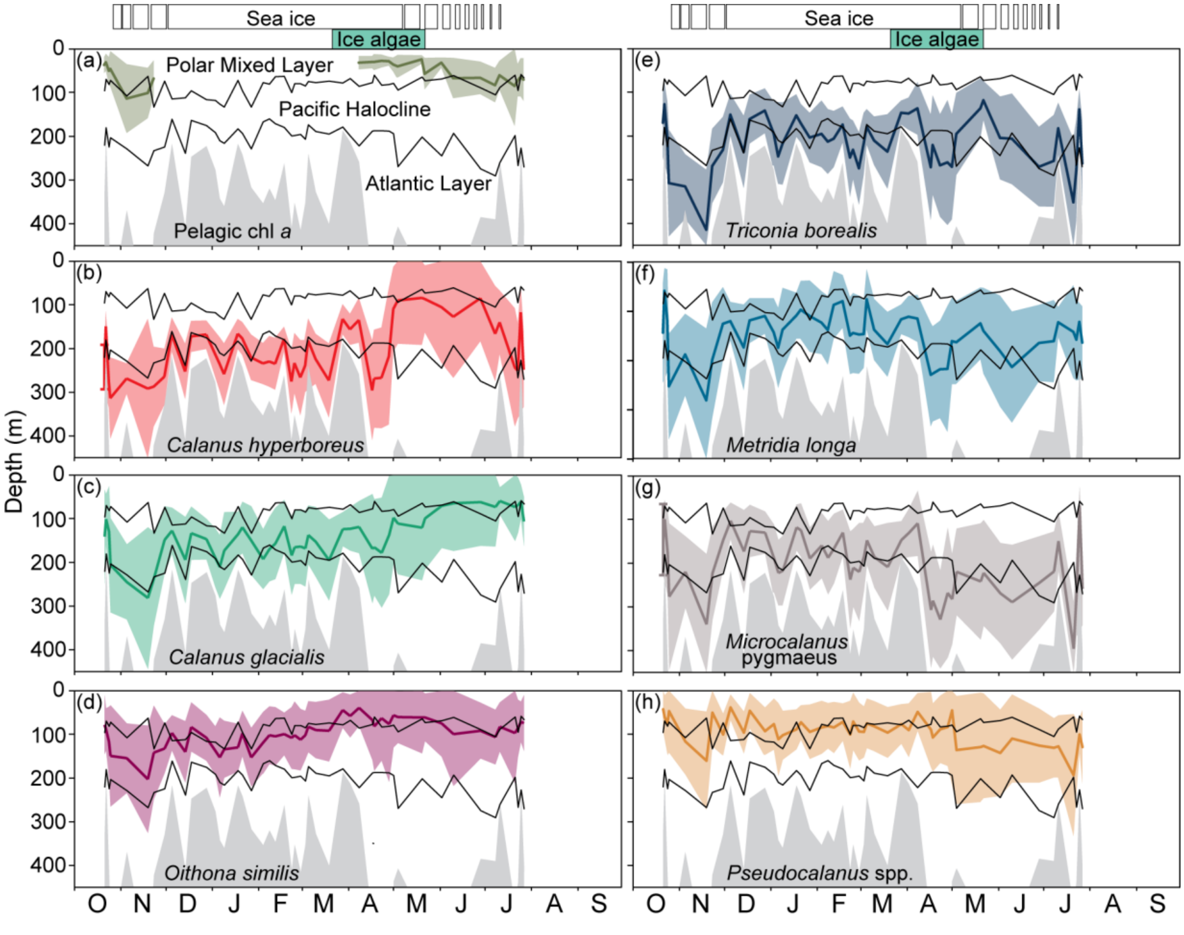


Figure 2.4. Time series of weighted mean depth (± 1 standard deviation) of pelagic chl *a* (a), and of each of the seven dominant copepod species (b-h) in the Amundsen Gulf from October 2007 to July 2008 (only the 66 stations inside Amundsen Gulf are included). The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer are repeated in each panel (fine lines).

From October to late April, most of the *Calanus hyperboreus* population occupied the deep Atlantic Layer below the 0ºC isotherm (Figure 2.4b). The winter residence depth tended to be deeper in the deep regions of Amundsen Gulf sampled in October, November and late April, and to follow bottom topography in the shallower region sampled from December to mid April. A brief incursion in the Pacific Halocline in late March and early April matched the onset of ice algae production. However, the rapid upward migration in late April responded to phytoplankton production (Figure 2.4a). In May and June, the distribution of *Calanus hyperboreus* spanned the Polar Mixed Layer and most of the Pacific Halocline, with the weighted mean depth (WMD) of the population located at the top of the Pacific Halocline just under the subsurface chlorophyll minimum (Figure 2.4a and b). The downward migration started in early July.

Calanus glacialis resided in the Pacific Halocline in winter, its WMD being located more often in the lower, warmer half of this layer (Figure 2.4c). The winter depth ranges of *C. glacialis* and *C. hyperboreus* overlapped in the lower part of the Pacific Halocline and the upper part of the Atlantic Layer (Figure 2.4b and c). The first sign of an upward vernal migration was detected in early April as the WMD of the population started to rise and some individuals entered the Polar Mixed Layer (Figure 2.4c). By late April, the distribution extended to the ice-water interface coincident with maximum ice algae production. In May and June, the WMD of *Calanus glacialis* matched precisely that of the subsurface chlorophyll maximum, just above the -1.6ºC isotherm. No clear sign of a downward migration had been detected by the end of sampling in late July.

The WMD of *Oithona similis* was located in the middle of the Pacific Halocline in October and November, and closely tracked the -1.6ºC isotherm from early December onward (Figure 2.4d). *O. similis* slowly rose into the Polar Mixed Layer from February to April, some animals reaching the ice-water interface in early April as ice algae first appeared. The WMD of the population was located just under that of the subsurface chlorophyll maximum in June and July.

The winter distribution of *Triconia borealis* in the Atlantic Layer (Fig. 4e) closely matched that of *Calanus hyperboreus* (Figure 2.4e). *T. borealis* followed *C. hyperboreus* in the cold <0ºC Pacific Halocline in May, but descended back to the 0ºC isotherm in June and July.

Metridia longa and *Microcalanus pygmaeus* exhibited little SVM, their WMD hovering between 100 and 300 m in all seasons (Figure 2.4f and g). Both species tended to distribute deeper (often in the Atlantic Layer) in the deep regions of Amundsen Gulf sampled in October, November and from late April to June, and to reside higher in the Pacific Halocline in the shallower region sampled from December to mid April.

Most of the population of *Pseudocalanus* spp. was distributed in a narrow band straddling the -1.6ºC isotherm in the cold sub-surface layer from December to May (Figure 2.4h). In May, the population rapidly spread to cover the entire Polar Mixed Layer and Pacific Halocline from the ice-water interface to the 0ºC isotherm. From May to July, the WMD of *Pseudocalanus* spp. was located under the subsurface chlorophyll maximum (Figure 2.4h).

2.5.4 Weighted mean depth and thermal regime by species and copepodite stage

***Calanus hyperboreus*.** CI and CII copepodites occurred primarily during the phytoplankton bloom from late May to mid June (Figure 2.5a), experiencing sub-zero temperatures (<0 to -1.6°C) and developing into CIII before any downward migration (Figure 2.5b). CIII to CV and females (F) exhibited a similar SVM, ascending from the same overwintering depth in the Atlantic Layer (October to March) to the surface layer in April-May, followed by a progressive descent starting earlier in F (May) than in CIV-V (June) or CIII (July) (Figure 2.5a-d). This pattern maintained CIII to F stages in the Atlantic Waters at zero or near-zero temperatures from October to April, before exposing them to the sub-zero (-1 to -1.7°C) temperatures of the Pacific Halocline and Polar Mixed layer during their vernal ascent towards the surface (Figure 2.5e-f). Some CIV, CV and F (but no CIII) occurred in the >0°C lens of warm water in June and July. Males remained in the deep and warm Atlantic Waters from October to early June before disappearing from the population (Figure 2.5d and h).

***Calanus glacialis*.** CI and CII appeared in July in the Polar Mixed Layer experiencing temperatures <-1°C on average, except during incursions into the >0°C lens of warm surface waters (Figure 2.6a and e). CI and CII persisted until January in the population, starting their descent into the lower part of the Pacific Halocline and the Atlantic Waters (0 to -1.5°C) sometime between late July and October. CIII to CV copepodites overwintered (October to March) in the lower part of the Pacific

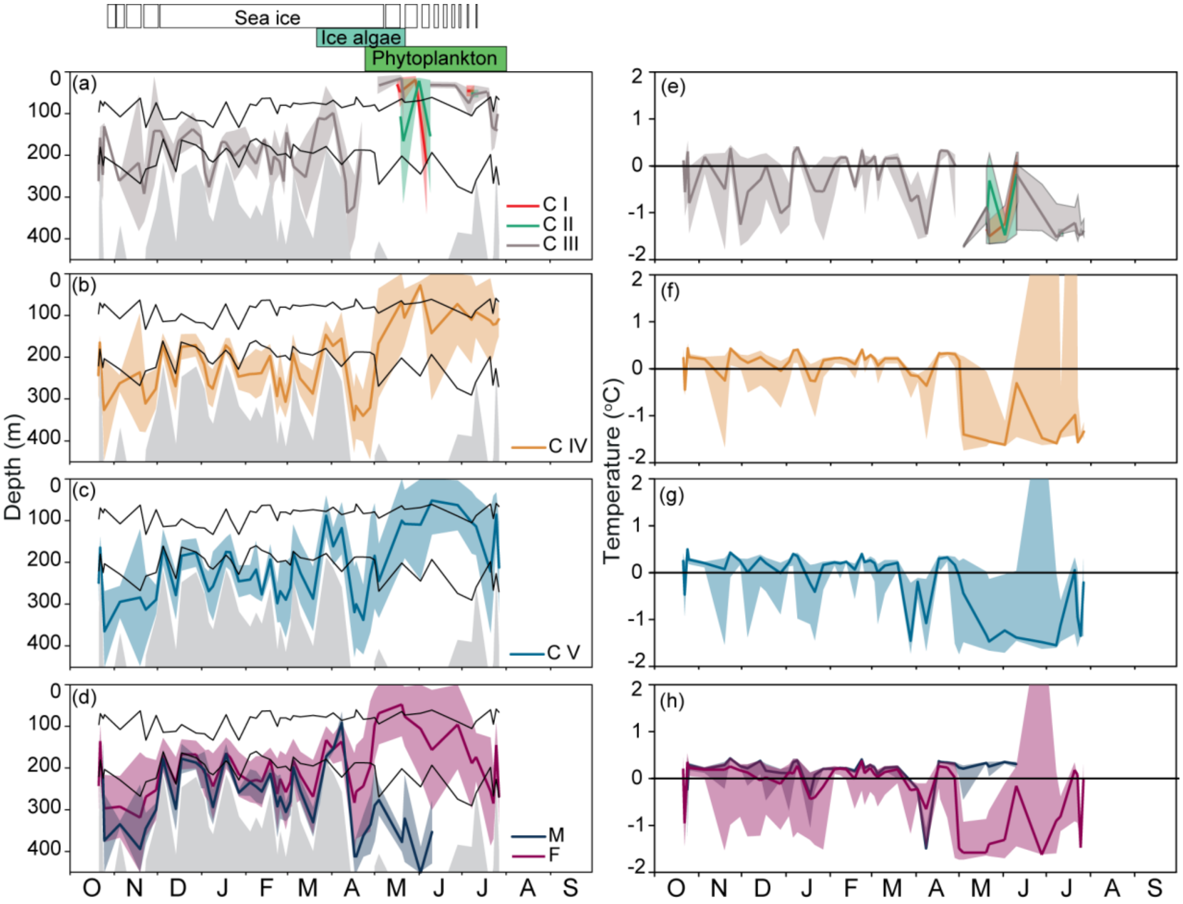


Figure 2.5. *Calanus hyperboreus*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-d), and corresponding water temperature prevailing at the WMD of each stage (e-h) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-d. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

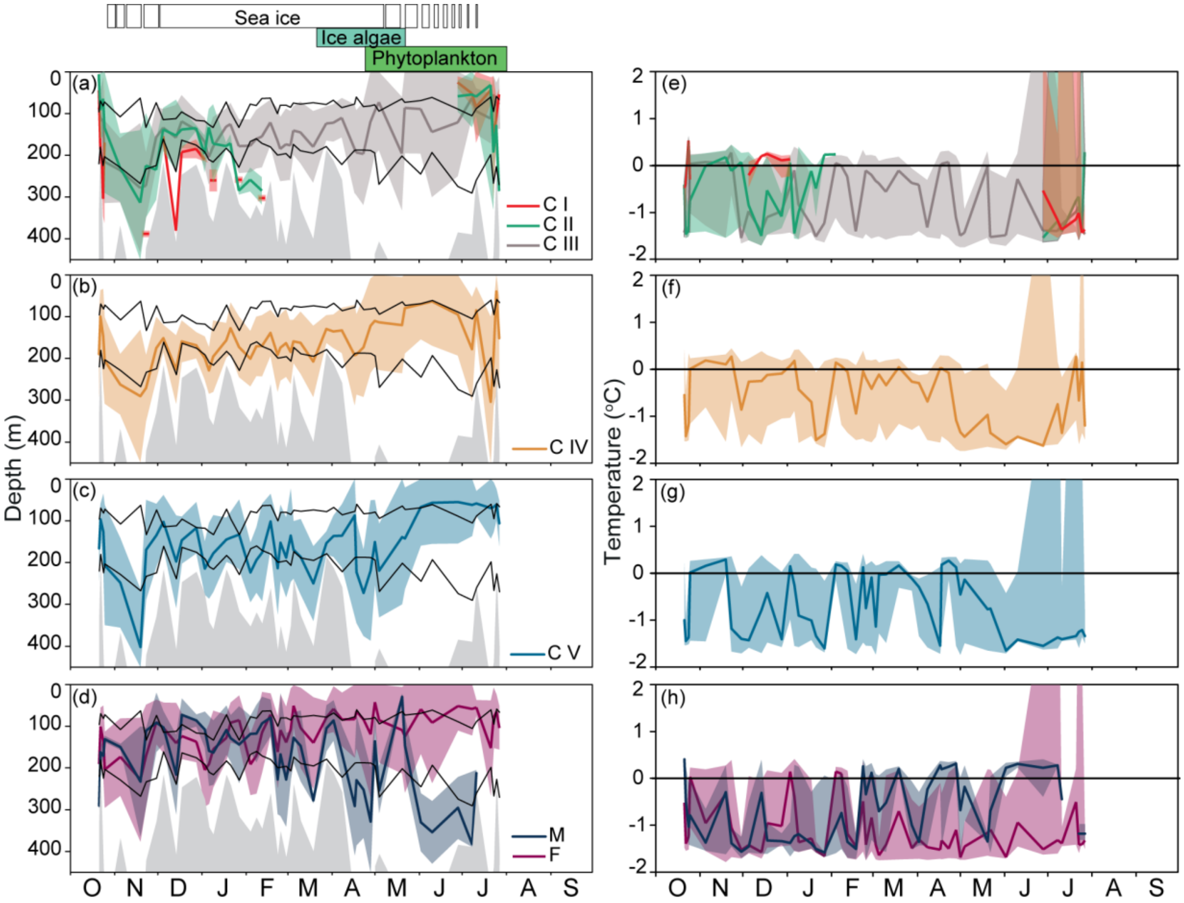


Figure 2.6. *Calanus glacialis*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-d), and corresponding water temperature prevailing at the WMD of each stage (e-h) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-d. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

Halocline and in Atlantic Waters, where they experienced temperatures ranging from 0 to -1.5°C, before invading the cold (<-1.5°C) waters of the upper Pacific Halocline and Polar Mixed Layer during the ice-algae and phytoplankton blooms from April to July (Figure 2.6a-c, e-g). Adults overwintered in the cold Pacific Halocline at sub-zero (-0.5 to -1.6°C) temperatures on average. The vertical distribution of both sexes coincided from October to February and then diverged as females ascended in Pacific Halocline from March to July, while males tended to descend in the Atlantic Waters (Figure 2.6d and h).

Oithona similis. The CI to CIII of this small species were poorly retained on the 200-µm mesh of our sampler (Figure 2.7a). CI and CII were collected sporadically from January to July, mainly in the Polar Mixed Layer, suggesting a protracted reproduction season. All stages from CIII to adults inhabited the Pacific Halocline in winter, slowly descending to half depth from October to January, and then progressively ascending from February to April to reach the Polar Mixed Layer in May at the onset of microalgal production (Figure 2.7b-d). The adults started their fall descent earlier (mid-June) than the CIII-CV (after July). This slow migration through the Pacific Halocline maintained all stages at cold average temperatures (ca. -1.5°C) throughout the year (Figure 2.7e-f).

Triconia borealis. Only the CV and adults of this small copepod were collected. Except for brief incursions higher in the Pacific Halocline in May-June (adults) and in July (CV), this species remained most of the time in the deep Atlantic Waters with sporadic occurrences in the Pacific Halocline (Figure 2.8a, b). Accordingly, all three stages experienced temperatures between 0 and -1.5°C throughout the year (Figure 2.8c, d).

Metridia longa. Except for two interruptions in late March and late April, CI and CII occurred throughout the year in our collections (Figure 2.9a). CI and CII descended from the base of the Pacific Halocline into progressively deeper Atlantic Waters from October to early May, and ascended back into the Pacific Halocline at the onset of the phytoplankton bloom. A similar SVM pattern but with lesser vertical amplitude was found in CIII, CIV, and CV, which distributed shallower with each moulting stage, from the Atlantic Waters (CIII) to the base of the Pacific Halocline (CV) (Figure 2.9b-d). As a result, CI to CIV copepodites experienced near-zero average temperatures (-0.3 to +0.3°C) from February to July, whereas CV were exposed to colder temperatures (<0 to -1.5°C) throughout the year (Figure 2.9f-i). Over the months, the adults oscillated between the Pacific Halocline and the Atlantic Layer, experiencing temperatures from slightly over zero to -1.5°C (Figure 2.9e and j). The males, which distributed consistently deeper than the females, were exposed to warmer temperatures on average.

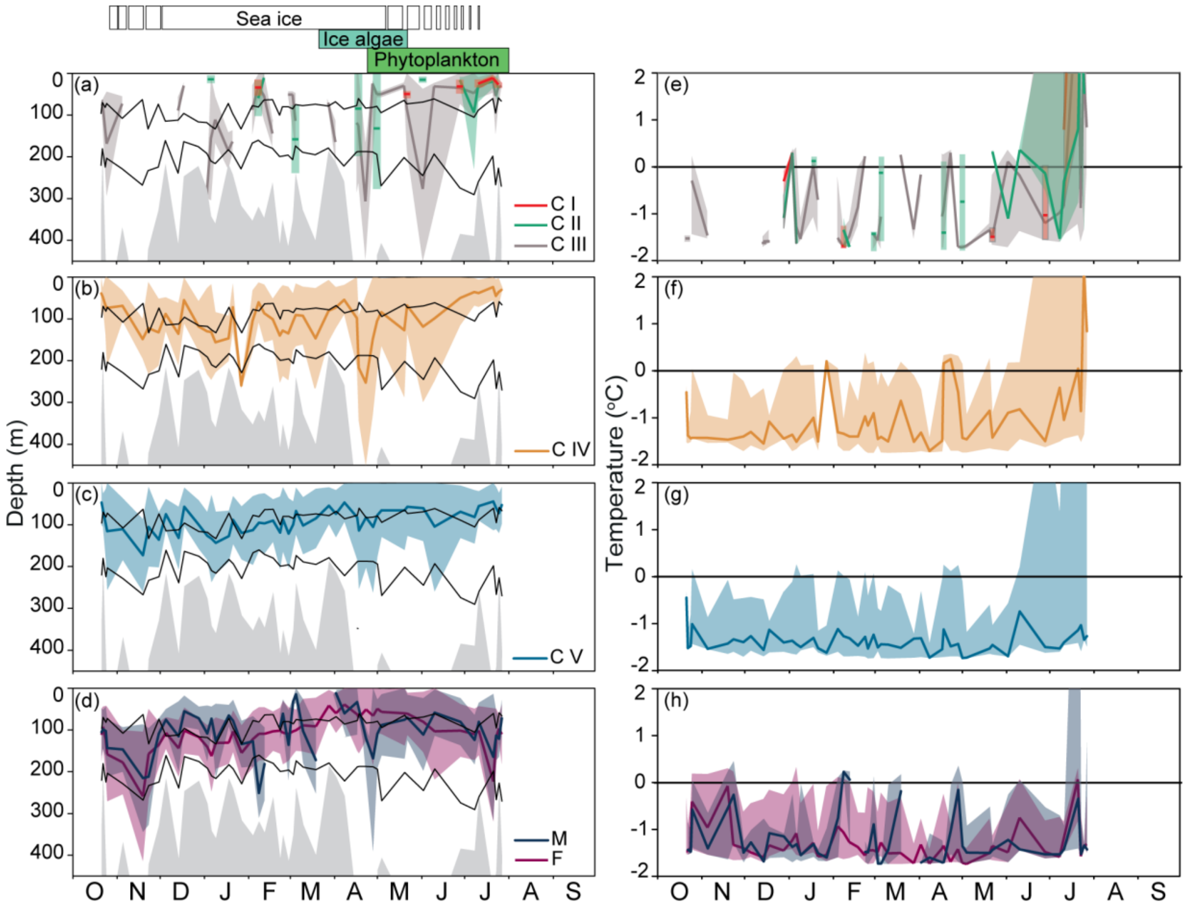


Figure 2.7. *Oithona similis*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-d), and corresponding water temperature prevailing at the WMD of each stage (e-h) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-d. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

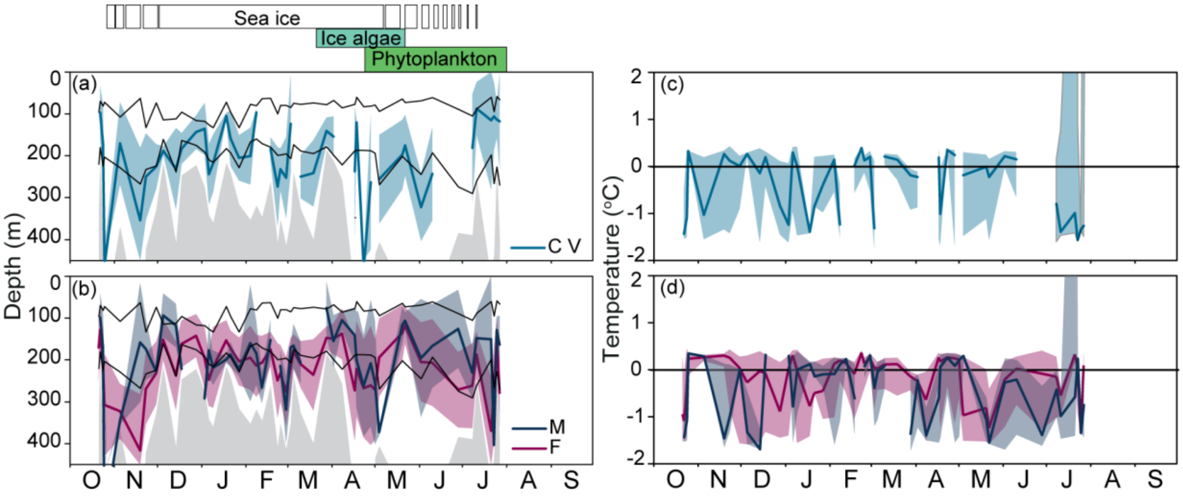


Figure 2.8. *Triconia borealis*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CV, Female and Male) (a-b), and corresponding water temperature prevailing at the WMD of each stage (c-d) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-b. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

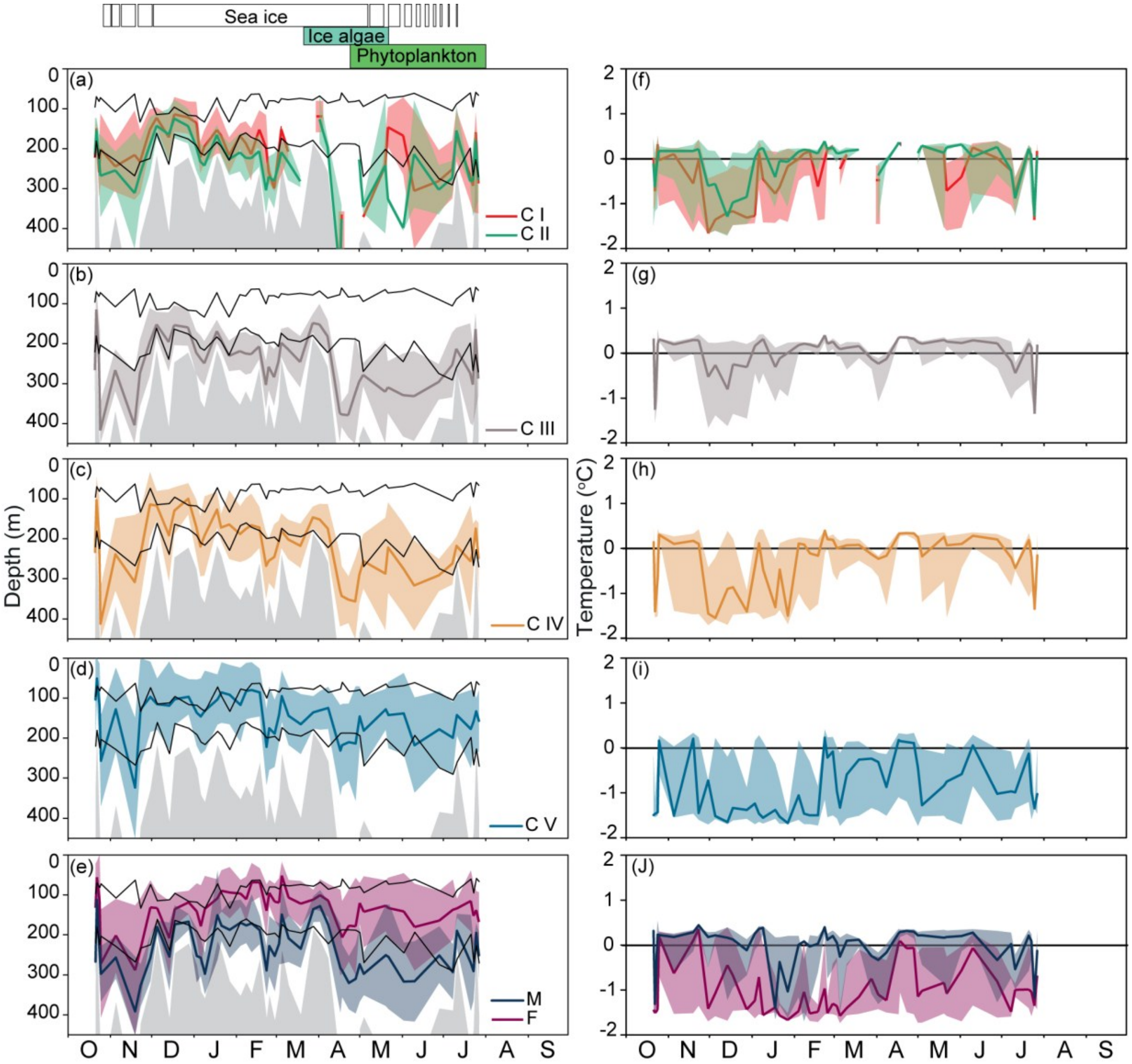


Figure 2.9. *Metridia longa*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-e), and corresponding water temperature prevailing at the WMD of each stage (f-j) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-e. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

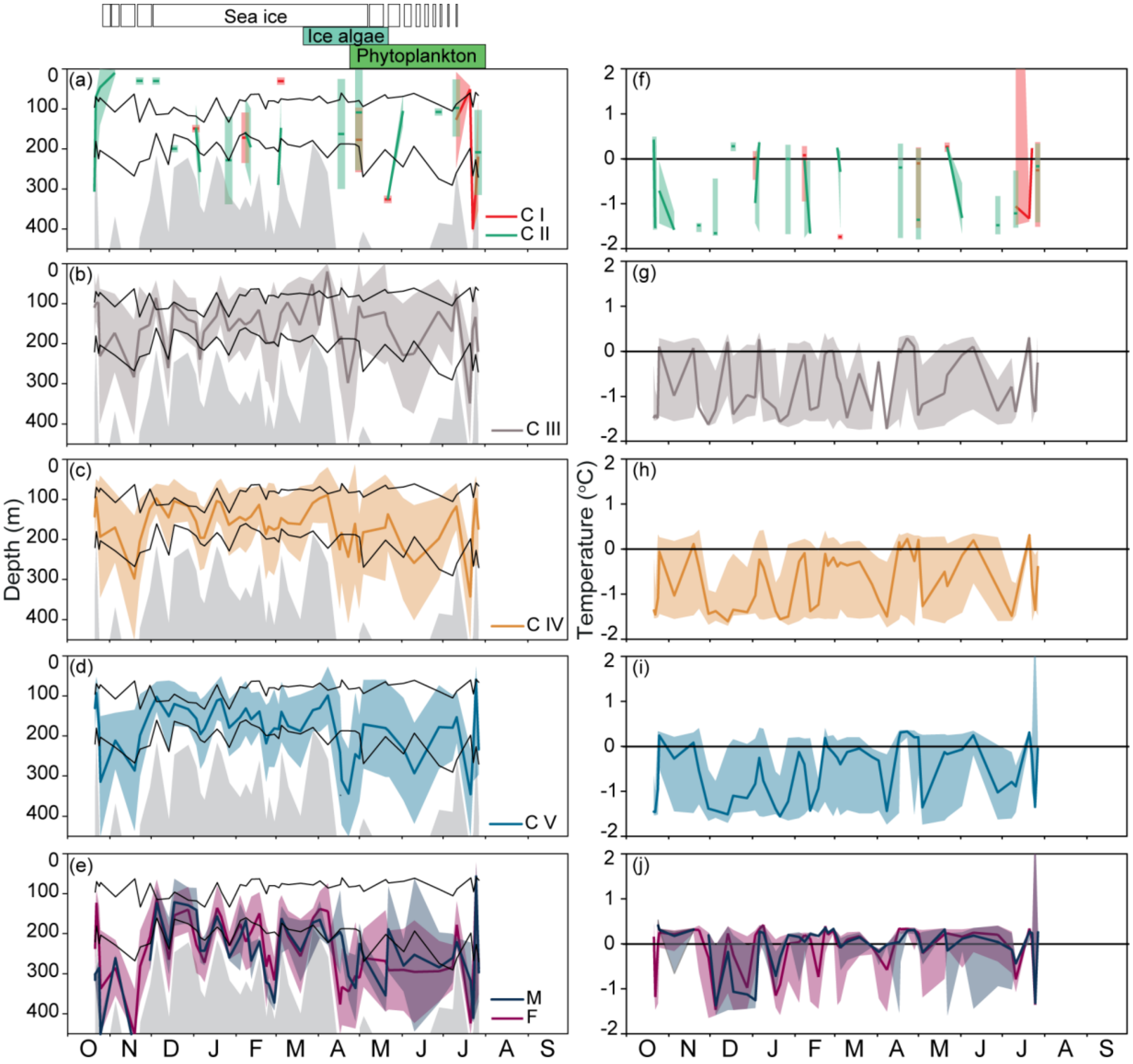


Figure 2.10. *Microcalanus pygmaeus*. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-e), and corresponding water temperature prevailing at the WMD of each stage (f-j) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-e. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

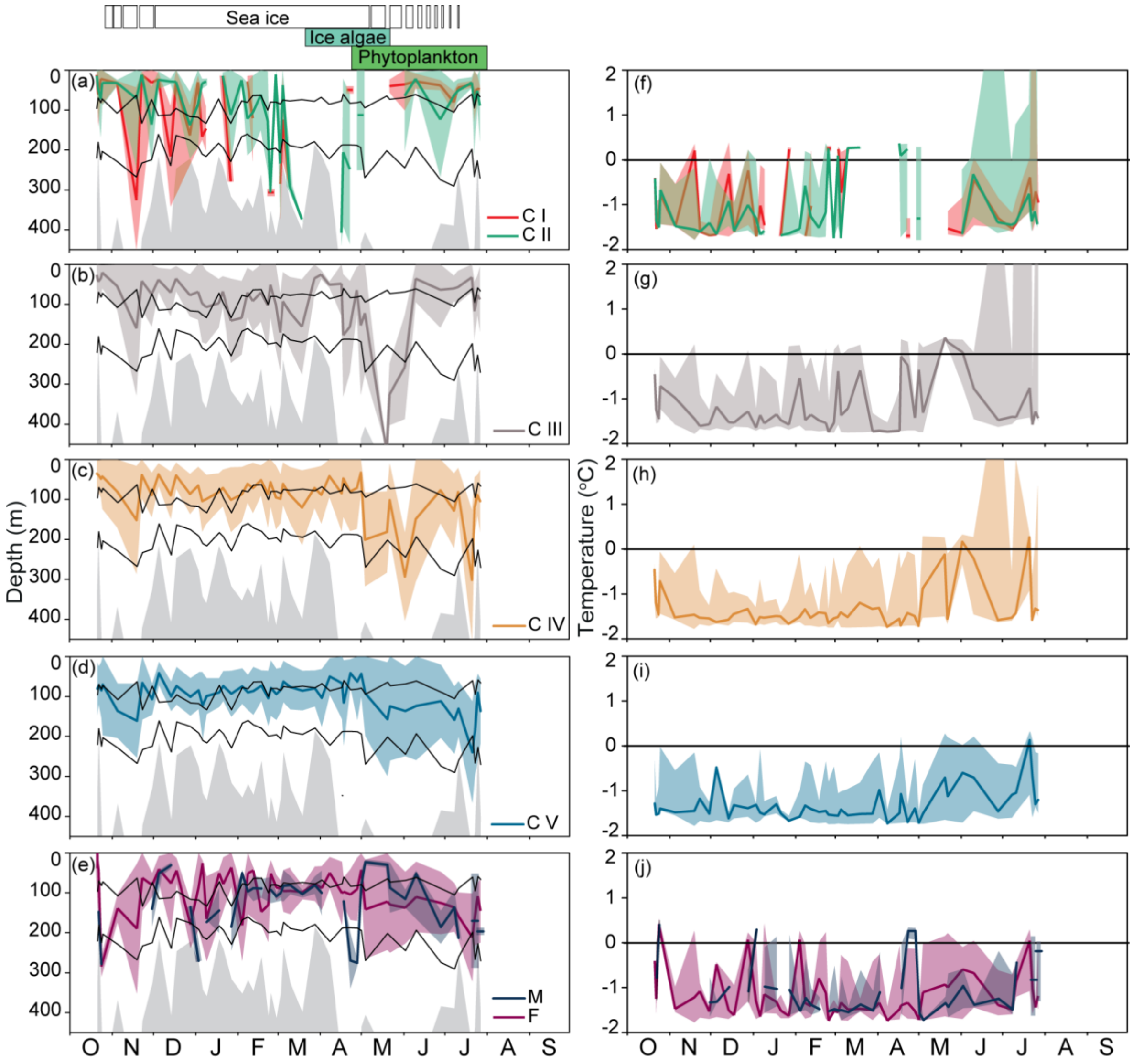


Figure 2.11. *Pseudocalanus* spp. Time series of weighted mean depth (WMD ± 1 standard deviation) of the biomass of copepodite stages (CI to CV, Female and Male) (a-e), and corresponding water temperature prevailing at the WMD of each stage (f-j) from October 2007 to July 2008 in Amundsen Gulf. The -1.6°C and 0°C isotherms marking respectively the boundary between the Polar Mixed Layer and the Pacific Halocline and between the Pacific Halocline and the Atlantic Layer (cf Figure 2.4a) are repeated in panels a-e. The area around the temperature at WMD indicates the temperature range over the depth distribution of each copepodite stage.

***Microcalanus pygmaeus*.** The small CI to CII, which were poorly retained on the 200-µm mesh of our sampler, occurred sporadically throughout the year (Figure 2.10a). This species presented no clear SVM pattern. CIII to CV hovered around mid-depth throughout the year (Figure 2.10b-d), generally exposed to the cold temperatures (<0 to -1.5°C) of the Pacific Halocline (Figure 2.10g-i). The adults were distributed deeper than the CIII to CV, experiencing slightly warmer (+0.3 to -1.0°C) temperatures (Figure 2.10e, j).

***Pseudocalanus* spp.** CI and CII were collected regularly from October to February and in June and July (Figure 2.11a). This species complex presented no clear SVM with all stages remaining in the cold waters (-1.6°C) of the upper Pacific Halocline and Polar Mixed Layer for most of the year (Figure 2.11). Some CII to CIV copepodites occurred in the warm lens of surface water in June and July (Figure 2.11f-h).

2.6. Discussion

2.6.1 Life strategies and the seasonal vertical migrations of migrating arctic copepods

Studies of the vertical distribution of arctic copepods at the scale of the annual cycle are few and have focused mainly on large calanoid herbivores that display strong seasonal vertical migrations (SVM). Early works noted that calanoids, in particular the large pelagic *Calanus hyperboreus*, were present in the surface layer during May and June only, and that all developmental stages congregated at depths that could exceed 1000 m from September to March (Østvedt 1955; Dawson 1978; Hirche 1997; Auel et al. 2003). Both *C. glacialis* and *Metridia longa* were found mostly in the top 200 m, with the former accumulating at the surface in summer and the latter remaining at all times distributed over the mesopelagic zone (Buchanan et Sekerak 1982; Longhurst et al. 1984; Groendahl et Hernroth 1986; Conover et Huntley 1991; Unstad et Tande 1991; Madsen et al. 2001). Smaller arctic species such as *Oithona similis* and the oncaeids, which are often omnivorous and cryptic, were suspected to distribute widely vertically and not to migrate over long distances (Conover et Huntley 1991; Vinogradov 1997). Perhaps the most complete study to date of arctic copepod SVM is that of Ashjian et al. (2003) who tracked the vertical distribution of five species during the drift of their ice camp from the Beaufort Sea to the Chukchi Sea over an annual cycle. Despite the confounding effect of a transition through 4 different oceanographic regimes, their observations confirmed the classical SVM pattern in *C. hyperboreus* and *C. glacialis*, and the relatively constant vertical distribution of *O. similis, Microcalanus pygmaeus* and *M. longa*.

In the present study, a classical seasonal vertical migration (SVM) was detected in *Calanus hyperboreus*, *C. glacialis*, and *Oithona similis* (Figure 2.3). The *Pseudocalanus* spp. complex exhibited some deepening of its epipelagic distribution in summer that may be interpreted as a SVM of modest amplitude. *Triconia borealis*, *Metridia longa*, and *Microcalanus pygmaeus* showed no clear seasonal vertical migration, variations in their vertical distribution being seemingly influenced primarily by local depth.

Calanus hyperboreus, most likely the only true herbivore copepod in the ecosystem (Forest et al. 2011a), occupied the Atlantic Layer in winter. Apparently, the bottom limited winter residence depth in shallow areas of Amundsen Gulf where the center of mass of the population hugged the seafloor (Figure 2.4b). *C. hyperboreus* exhibited the widest SVM of all seven species, moving rapidly from the Atlantic Layer, across the Pacific Halocline and to the base of the Polar Mixed Layer in late April, at the time when phytoplankton first became detectable in the surface waters. The envelop of the distribution (as defined by one standard deviation of the WMD) reached the ice-water interface in early May as the ice algae bloom declined. The upward migration was completed on time to coincide with the intensification of the phytoplankton bloom which, in 2008, occurred one month earlier than typical because of the unusually early ice break-up in Amundsen Gulf (Galley et al. 2008). The production of ice algae may be important for the first feeding naupliar stages that accumulate under the ice after hatching from buoyant eggs spawned at depth in winter (Conover et Huntley 1991). However, the timing of the vernal ascent of CIII to CV and adults suggests that they rely mostly on phytoplankton and little on ice algae to fuel their carbon demands (Figure 2.5). *C. hyperboreus* is particularly efficient at extracting lipids from the pelagic diatom bloom (Falk-Petersen et al. 2009). Females initiated the downward migration in July followed in succession by the CV, CIV and CIII, which suggests that, as they develop, copepodites need less and less time in the surface layer to extract the quota of lipids needed to overwinter. Assuming conservatively that the downward migration was completed in August (not sampled in this study), CIII to adult females spent over 7 months of the year (September to March) at depth, as reported for the Arctic Ocean deep basins (Dawson 1978; Ashjian et al. 2003). Males remained at depth from October to March, slightly deeper on average than females, did not participate in the vernal migration, and vanished from the population in early June (Figure 2.5d). Solely fuelled by lipid reserves, reproduction spanned four months (January to April), peaking in March with the release of large numbers of lipid-rich buoyant eggs in the deep layers of Amundsen Gulf (Chapter 3), which resulted in high concentrations of nauplii in the water column at the same period (Darnis et al. 2012). The carcasses of female *C. hyperboreus* that likely died of senescence after reproduction contributed heavily to a maximum in POC flux at the mouth of Amundsen Gulf in February 2008 (Sampei et al. 2012). These may represent an important food source for other zooplankton and microbes in the absence of primary production.

Calanus glacialis is an herbivore with some omnivorous proclivity (Campbell et al. 2009; Forest et al. 2011b). In spring, it hastens maturation and egg production by feeding on ice microalgae at the ice-water interface, but the phytoplankton bloom remains the primary fuel for reproduction (Runge et Ingram 1991; Tourangeau et Runge 1991; Soreide et al. 2010; Wold et al. 2011). Dense aggregations of late copepodite stages and females were observed in June 2008 in the melt water layer immediately under the landfast ice of Franklin Bay (Hop et al. 2011). Consistent with earlier reports (see Conover and Huntley 1991 for a review), the epipelagic *C. glacialis* remained in the Pacific Halocline mainly above 200 m in the Amundsen Gulf in winter. The spring ascent started with the ice diatom bloom in early April. However, as in *C. hyperboreus*, the envelop of the distribution first reached the ice-water interface in early May after the ice algae bloom had started to decline. All copepodite stages remained on average at the base of the Polar Mixed Layer from April to the end of the study in July, presumably feeding on the subsurface chlorophyll maximum. CI and CII occurred from late June until January, indicating that egg production continued late into the summer, consistent with the persistence of females in the subsurface chlorophyll maximum (Figure 2.6d). Males remained at depth in summer, but egg fertilization in the surface layer was nevertheless possible as females carry spermathecae. Despite their relatively small size, *C. glacialis* CI and CII (0.6-1.4 mm prosome length) partook in the downward migration to overwintering depths (Figure 2.6a). By comparison, by completing spawning well before the onset of microalgal production (Chapter 3), *C. hyperboreus* provided its CI and CII with enough time to mature into overwintering CIII before leaving the surface layer (Figure 2.5a).

Contrary to expectations, the ubiquitous epipelagic omnivore *Oithona similis* exhibited a modest but clear SVM, its distribution spreading over the Pacific Halocline from October to March, after which most of the population congregated in the Polar Mixed Layer (Figure 2.3c). From November onward, the center of mass of the population roughly tracked the PML-PH border (Figure 2.4c). *O. similis* was the first migrant copepod to reach the ice-water interface at the end of March, only days after the first signs of ice algae production. This species accumulates limited lipid reserves (Narcy et al. 2009) and reproduces throughout the year (e.g. Ashjian et al. 2003). Which raises the question of wintertime feeding when the animals are distributed mainly in the cold and oligotrophic waters of the Pacific Halocline (Figure. 2.4c). Part of the metabolic needs may be met by preying on heterotrophic dinoflagellates and ciliates at the top of an active winter microbial food web sustained by a low but steady production of bacteria (Darnis et al. 2012). Knowledge of the overwintering vertical distribution of heterotrophic protists could be useful in interpreting the gradual winter ascent of *O. similis* through the Pacific Halocline from November to March.

In Amundsen Gulf, the *Pseudocalanus* spp. complex was the most epipelagic of the seven taxa studied. From October to April, its narrow vertical distribution bestrode the -1.6°C isotherm separating the Polar Mixed Layer and the Pacific Halocline (Figure 2.4h). Like *Oithona similis*, *Pseudocalanus* spp. accumulates modest lipid reserves and the complementary energy sources needed to fuel its metabolism in winter remains unidentified. Like *Calanus glacialis*, female *Pseudocalanus* have been reported to ascend to the ice-water interface in spring to graze ice algae sloughing from the bottom of the landfast ice (Conover et al. 1986; Runge et Ingram 1991). Contrary to expectation and at odd with *Calanus hyperboreus*, *C. glacialis* and *O. similis*, *Pseudocalanus* spp. only sporadically reached the ice-water interface during the ice algae bloom (Figure 2.4h). From May to July, a spread of the distribution over most of the Pacific Halocline brought the larger CV and adult females under the subsurface chlorophyll maximum (Figure 2.11b-e). In temperate seas, fish larvae and juveniles often select the relatively abundant, conspicuous and weakly protected egg-carrying females of *Pseudocalanus* to maximize energy intake per attack (see review by Robert et al. 2011). In spring and summer, the larvae and juveniles of the Arctic cod (*Boreogadus saida*) and other fishes prowl the surface layer of the Amundsen Gulf (Geoffroy et al. 2011). Hence, the avoidance of visual predators in the surface layer, the deepening of the SCM, the warming of the near-surface layer or a combination of these factors could explain the ontogenetic short-range downward migration of *Pseudocalanus* spp. in May (Renz et Hirche 2006).

2.6.2 The vertical distribution of non-migrating arctic copepods

Triconia borealis was the only copepod of the guild co-residing with *C. hyperboreus* in the Atlantic Layer in winter (Figure 2.2). The feeding ecology of this minuscule copepod remains mysterious. Its fatty acid and alcohol composition point to omnivory and/or semi-parasitism to carnivorous animals feeding on copepods (Kattner et al. 2003). Interestingly in this context, the intense production of *T. borealis* nauplii in February 2008 (Darnis et al. 2012) coincided with the massive sinking of female *C. hyperboreus* carcasses (Sampei et al. 2012). Starting in April, a brief incursion above the 0°C isotherm coincided with the upward migration of *C. hyperboreus*, as if limited swimming capacity due to a small size or the cold waters of the Pacific Halocline discouraged *T. borealis* from following *C. hyperboreus* towards the surface (Figure 2.4). These observations are consistent with the notion that the deep-dwelling *T. borealis* is a detritivore living off the faecal pellets and carcasses of copepods, in particular that of *C. hyperboreus*, and perhaps the discarded houses of appendicularians as observed in other oncaeids (Ohtsuka et al. 1993)

Consistent with their status of mesopelagic copepods (Auel et Hagen 2002; Ashjian et al. 2003), *Metridia longa* and *Microcalanus pygmaeus* remained in the Pacific halocline and upper Atlantic Layer year-round. Changes in the similar vertical distribution of both species were more closely related to station depth than season, the animals hovering about mid depth in basins >400 m deep and closer to the bottom in the shallower region sampled from late November to April (Figure 2.4f and g). Hence, these vertical movements can hardly be interpreted as a SVM. Ranked third in the order of dominance of mesozooplankton (Forest et al. 2008; Chapter 4), *M. longa* is an important omnivore/detritivore that feeds on a large range of food items (Haq 1967). The considerable amounts of buoyant eggs released by female *Calanus hyperboreus* in winter constitute a prime food resource for the late stages of *M. longa* prior to the onset of pelagic primary production (Darnis et al. 2012). Coherent with the report of Conover and Huntley (1991), the gut of a large number of female *M. longa* turned orange after gorging on eggs in late March 2008 at the peak of the reproduction of *C. hyperboreus*. Interception of these coloured eggs rising to the surface likely triggered the reproduction of *M. longa* in late March (Chapter 3). In April, stable isotope analysis showed that the late stages of *M. longa* switched to herbivory, feeding on sinking ice algae (Forest et al. 2011a). Information on the diet of *Microcalanus pygmaeus* in arctic waters is rudimentary but the morphology of its mouthparts, similar to those of *Metridia*, suggests that it feeds on phytoplankton and zooplankton (Michels et Schnack-Schiel 2005). The similar mouthparts and vertical distributions suggest that *M. pygmaeus* could share the feeding strategy of *M. longa* despite the difference in body sizes. Hence, the two species could be characterized as mid-depth interceptors, feeding on the upward flux of *C. hyperboreus* eggs in late winter-early spring and on the rain of microalgae in spring-summer.

2.6.3 Temperature regimes of migrant and non-migrant copepods in the thermally stratified Arctic Ocean

Over the temperature range -1.7 to 30.7ºC, the estimated growth rate (n = 181) of 33 copepod species increased exponentially with temperature, which explained over 90% of growth rate variations (Huntley et Lopez 1992). This strong dependence of growth on temperature led Huntley and Lopez (1992) to hypothesize that food may not be limiting to copepod growth in nature. Except for a brief warming of the surface layer in summer (typically 2-8ºC), cold temperatures prevail most of the time in Arctic seas, from the freezing point (~ -1.8ºC) in the surface Polar Mixed Layer to 0 to 0.3ºC in the deep Atlantic Layer. At these low temperatures, all species could be expected to seek the warmest available temperature if their life strategy aims at maximizing growth, maturation and reproduction.

In the present study, except for *C. hyperboreus* CI and CII that turned into CIII within the surface layer in summer and male *Calanus* that did not participate in the migration, all the copepodite stages of seasonally migrating species (*C. hyperboreus, C. glacialis, O. similis,* and perhaps *Pseudocalanus* spp.) migrated simultaneously and were found together at a given depth in a given season (Figure 2.5, 2.6, 2.7, 2.11). Hence, the different copepodite stages of a migratory species experienced roughly the same temperature regime during the simultaneous SVM. By contrast, the copepodite stages of the non migrating *Metridia longa* and *Microcalanus pygmaeus* each occupied a different depth interval throughout the year, which resulted in different temperature history among stages (Figure 2.9 and 2.10).

Contrary to expectation, we found little evidence that arctic copepods systematically sought warm waters. All copepodite stages of non-migrating copepods (*Triconia borealis*, *Metridia longa* and *Microcalanus pygmaeus*) generally avoided the warm summer surface lens, whereas only a fraction of the population of migrating copepods (*Calanus hyperboreus*, *Calanus glacialis*, *Oithona similis* and *Pseudocalanus* spp.) entered it in June and July, the weighted mean depth of migrating species remaining well below the warm surface waters (Figure 2.5-2.11). Hence, for most of the year, the copepodite stages of all species lived in the remaining narrow temperature range from -1.6 to +0.3ºC (Figure 2.2b).

Within this narrow range, only *Calanus hyperboreus* and its suspected semi-parasite *Triconia borealis* strove for the relatively warm Atlantic Layer (0 to 0.3ºC). Females of the large lipid-bearer *C. hyperboreus* may seek warmer waters in winter to hasten the maturation of eggs for their early release in March (Chapter 3). However, CIII to CV, which only mature and molt in spring when microalgal food is available (Chapter 3), would also waste precious energy to fuel a faster metabolism in the relatively warm waters of the Atlantic Layer in winter, suggesting that other factors such as visual predator avoidance push these large and lipid-rich copepodites in the dark Atlantic Layer. On average for this species, the vernal upward migration towards the subsurface chlorophyll maximum meant a transition to the frigid waters (-1.6ºC) of the Pacific Halocline for up to three months (Figure 2.5).

The mean depth of copepodite and adult of the relatively eurythermal *Calanus glacialis* oscillated widely within the temperature gradient (0 to -1.6ºC) of the cold Pacific Halocline (Figure 2.6). The seemingly more cryophilic *C. glacialis* spawns later than its congener *C. hyperboreus,* and may not need to hasten egg maturation by inhabiting the warm Atlantic Layer, as egg production in spring/summer is fuelled by both lipid reserves and grazing (Hirche et Kattner 1993).

By straddling the -1.6ºC at the boundary between the Polar Mixed Layer and the Pacific Halocline throughout the year, the cryophilic *Oithona similis* and *Pseudocalanus* spp. inhabited the coldest waters available in the Beaufort Sea (Figure 2.7 and 2.11). In these species that bear little lipid reserves, seeking low temperatures in winter may represent a strategy to reduce metabolism during months of presumably low food availability (Ingvarsdóttir et al. 1999).

Finally, the omnivores *Metridia longa* and *Microcalanus pygmaeus* exhibited no sign of an active seasonal vertical migration, but the different depth intervals occupied in succession by their copepodite stages resulted in clear ontogenetic migrations. Except in December, the deep-dwelling CIII and male *M. longa* enjoyed a balmy -0.3 to +0.3ºC between the Atlantic Layer and the Pacific Halocline, whereas CIV, CV and female experienced increasingly cold temperatures (down to -1.6ºC) during their ontogenetic progression into the Pacific Halocline (Figure 2.9). The ontogenetic migration of *M. pygmaeus* was in the opposite direction, the young stages (CI to CIII) residing in the cold Pacific Halocline and the CV and adults moving into the warm Atlantic Layer (Figure 2.10). The exogenous or endogenous factor(s) forcing the ontogenetic migration of these omnivore copepods remain purely speculative. However, optimal foraging theory predicts that if food is limiting and/or foragers interfere (e.g. through competition for food or cannibalism), the foraging animals will spread in proportion to resource availability so as to minimize competition and maximize individual gain in energy (e.g. Fortier et Harris 1989). Which suggests that the stage-dependent partitioning of the water column by each species could be a strategy to share a limited food resource.

Contrary to expectations, the temperature preferenda of the seven species ranged from the coldest to the warmest waters available in Amundsen Gulf. Except perhaps for *Calanus hyperboreus*, the vertical migrations and distributions of the different species showed no evidence of being dictated by a need to maximize growth and/or reproduction in warmer waters. A possible explanation for this lack of appeal for warmer waters could be that the potential gain in growth in the range of temperature available to copepods in Amundsen Gulf is small. If we include the lens of warm surface water in June and July, this range (-1.7 to 8ºC) corresponds to the initial segment of the exponential relationship linking instantaneous growth rate G to temperature T, ($G = 0.0445e^{0.111T}$, Huntley and Lopez 1992). Over that initial segment, growth increases relatively slowly with increasing temperature. Nevertheless, between -1.7 ºC ($G = 0.0369$ d^{-1}) and 8ºC ($G = 0.1082$ d^{-1}), copepods would nearly triple their instantaneous growth rate and cut their generation time τ from 158 to 49 d ($\tau = 128.8e^{-0.120T}$, Huntley and Lopez 1992). In 2008, the lens of warm surface water occurred from at least mid June to the end of July and probably into August as well (Figure 2.2b), long enough for copepodites occupying it to accelerate substantially their growth and development. Several copepodite stages of 5 of the 7 species occurred in the warm lens (CI to CV *Oithona similis*; CV and M *Triconia borealis*; CII-CIV *Pseudocalanus* spp.; CI to F *C. glacialis*; CIV-CV-F *Calanus hyperboreus*), suggesting that the transition from sub zero to warm temperatures was possible physiologically. However, such incursions into the warm lens were brief (typically <2 weeks) and all indications are that only a small fraction of the stage population was involved as the mean depth of the distribution was invariably located in the cold waters at the base of the Polar Mixed layer or in the Pacific Halocline (Figure 2.5, 2.6, 2.7, 2.8, and 2.11). Thus, none of the species studied maximized its growth and development by exploiting the warm summer surface layer.

According to the equations of Huntley and Lopez (1992), G varied potentially from 0.0369 to 0.0460 d^{-1} and generation duration from 158 to 124 d between the extremes of the temperature range actually occupied by the seven species (-1.6 to +0.3ºC). Apparently, such temperature-dependent potential gains in growth and development rates were too modest to force all copepods into the warm Atlantic Layer, each species adopting a unique pattern of vertical migration and distribution resulting in widely variable temperature histories.

2.7. Conclusion

Two main strategies of vertical migration/distribution emerge from our study of the dominant seven species of arctic copepods. First, the classical SVM of migrating species that actively seek their microalgal food in or at the base of the Polar Mixed Layer in spring and summer. The winter residence depth, and hence the amplitude of the migration, generally increased with species body size and capacity to store lipids (>200 m in the large *Calanus hyperboreus*; 150-200 m in the intermediate *C. glacialis*; 100-150 m in *Oithona similis*; and <100 m in *Pseudocalanus* spp.), a trend also noted for the amplitude of the DVM of arctic copepods (Fortier et al. 2001). While the large *Calanus* congeners rely on vast lipid reserves to overwinter at depth, the energy source(s) that enable the small omnivores *O. similis* and *Pseudocalanus* spp. to survive and even reproduce in the cold unproductive waters of the Polar Mixed Layer and Pacific Halocline in winter remain conjectural.

The second strategy is the ambush strategy practiced by the mid-depth interceptor *Metridia longa*, which prey on the ascending eggs of *C. hyperboreus* in early spring and graze on sinking microalgal cells in spring-summer. Presumably, *Microcalanus pygmaeus* share this strategy with *M. longa*. The sharing of a limited food resource could perhaps explain the ontogenetic vertical partitioning of the water column among the copepodite stages of each species. A variant of this strategy is presented by the small *Triconia borealis*, which is believed to await close to the bottom the sinking carcasses of *C. hyperboreus* and other animals.

We found little evidence that, within the temperature range occupied most of the year by most of the populations/stages (-1.7 to +0.3ºC), temperature preferences or tolerance limited the vertical migration or distribution of any of the seven species, which readily moved across the vertical temperature gradient. On the contrary, it appeared that the different patterns of seasonal vertical migration of *Calanus hyperboreus*, *C. glacialis*, *Oithona similis* and *Pseudocalanus* spp., as well as the different ontogenetic migrations of *Metridia longa* and *Microcalanus pygmaeus* dictated the temperature regime experienced over the annual cycle by each species and copepodite stage. Growth and development are strongly dependent on temperature in copepods (Forster et al. 2011), and the detailed information provided here for the different copepodite stages should prove useful in models of the impact of changing temperatures on the growth, development and survival of these key arctic copepods.

3. Chapitre 3 – Life strategy and reproduction of the arctic copepod *Calanus hyperboreus* during a year of record-low ice cover in the southeastern Beaufort Sea

3.1. Résumé

Le cycle vital et la reproduction de *C. hyperboreus* ont été étudiés d'octobre 2007 à juillet 2008 pendant une année record de minimum de glace dans le sud-est de la mer de Beaufort. Les stades CIV, femelles adultes et CV ont dominé la population hivernante, suggérant un cycle annuel de 2 à 3 ans. Ils ont hiverné en profondeur jusqu'en avril et sont montés rapidement à la surface avant la fonte de la glace en mai et l'efflorescence du phytoplancton un mois plus tôt que la normale. En l'espace de deux mois, les femelles ont engrangé leurs réserves énergétiques, et ont initié leur migration saisonnière descendante en juillet. De février à mars, une reproduction vigoureuse (20-65 œufs f^{-1} j^{-1}) a apporté de nombreux œufs (28863 ± 23310 œufs m^{-2}) et nauplii NI-NIII (17097 ± 12257 ind. m^{-2}) dans la colonne d'eau. Toutefois, le recrutement de CI en mai, simultanément avec l'efflorescence phytoplanctonique, a été modeste (13-21% des copépodites) dans le golfe d'Amundsen par rapport à des sites en dehors du golfe (>75%). En conséquence, l'abondance et la biomasse de *C. hyperboreus* ont stagné pendant l'été dans le golfe d'Amundsen. Comme un décalage entre les premiers stades qui s'alimentent et la nourriture est improbable dans les conditions d'alimentation favorables d'avril-mai 2008, la prédation sur les jeunes stades à la fin de l'hiver a probablement limité le recrutement subséquent et la croissance de la population. Particulièrement abondant dans le golfe, le copépode *Metridia longa* a possiblement été un consommateur majeur des œufs et nauplii de *C. hyperboreus.* Avec l'allongement en cours de la saison libre de glace sous l'influence des changements climatiques, une intensification du contrôle descendant sur le recrutement de *C. hyperboreus* par des populations florissantes d'omnivores mésopélagiques comme *M. longa* pourrait contrecarrer les bénéfices potentiels d'une augmentation de la production primaire à la marge des plateaux continentaux arctiques.

3.2. Abstract

The life cycle and reproduction of *C. hyperboreus* were studied from October 2007 to July 2008 during a period of record low ice cover in the southeastern Beaufort Sea. Stages CIV, adult females and CV dominated the overwintering population, suggesting a 2- to 3-year life cycle. They overwintered at depth until April and made a fast ascent to the surface before the May ice melt and phytoplankton bloom, one month earlier than usual. Within two months, females filled their energy reserves and initiated their downward seasonal migration in July. From February to March, vigorous reproduction (20-65 eggs f^{-1} d^{-1}) brought numerous eggs (28,863 ± 23,310 eggs m^{-2}) and nauplii NI-NIII (17,097 ± 12,257 ind. m^{-2}) in the water column. However, CI recruitment in May, coincident with the phytoplankton bloom, was modest (13-21% of copepodites) in Amundsen Gulf compared to sites outside the gulf (>75%). Consequently, *C. hyperboreus* abundance and biomass stagnated throughout summer in Amundsen Gulf. As a mismatch between the first-feeding stages and food was unlikely under the favorable feeding conditions of April-May 2008, predation on the young stages in late winter presumably limited subsequent recruitment and population growth. Particularly abundant in Amundsen Gulf, the copepod *Metridia longa* was likely a main consumer of *C. hyperboreus* eggs and nauplii. With the ongoing climate-driven lengthening of the ice-free season, an intensification of top-down control of *C. hyperboreus* recruitment by thriving populations of mesopelagic omnivores like *M. longa* could counteract the potential benefits of increased primary production over the Arctic shelves margins.

3.3. Introduction

Throughout the past 30 years, the downward trend in minimum sea ice extent at the end of the melt season in September has continued to steepen, from a -9% per decade decline during the period 1979-2000 (Comiso 2002) to -12.9% when the satellite record is extended to 2011(Stroeve et al. 2012b). As sea-ice variability is a major structuring factor of the Arctic marine ecosystem, the climate-driven dramatic decline in ice-cover extent is bound to have serious implications for all levels of the trophic web (Darnis et al. 2012). Already, a 20% increase in phytoplankton annual net primary production over the Arctic Ocean and its marginal seas between 1998 and 2009 was largely driven by the lengthening of the growth season (+45 days) (Arrigo et van Dijken 2011). Zooplankton of the genus *Calanus* can be expected to respond positively to such rise in pelagic primary production, particularly in the coastal areas prone to upwelling (Tremblay et al. 2011). However, from 2004 to 2008 when summer sea ice declined severely in the Canada Basin, primary production remained constant while a shift in phytoplankton size toward small picophytoplankton was linked to stronger stratification and reduced nutrient load in the euphotic layer (Li et al. 2009). This change likely benefited small copepods and microphagous zooplankton over the large suspension feeders *Calanus glacialis* and *C. hyperboreus* (Tremblay et al. 2012b).

The oceanic copepod *Calanus hyperboreus* constitutes the prime herbivore in the Arctic Ocean and deep margins of its shelf seas where it dominates mesozooplankton biomass (Auel et Hagen 2002; Ringuette et al. 2002; Kosobokova et Hirche 2009; Darnis et Fortier 2012). This endemic species has developed specialized life-history strategies to adapt to a short and unpredictable season of food supply constrained by the variable timing of ice melt (Falk-Petersen et al. 2009). It performs a long-range seasonal migration to spend the cold and dark overwintering season of up to 10 months in diapause at depths sometimes exceeding 1000 m (Dawson 1978; Hirche 1997; Ashjian et al. 2003). Without food, winter reproduction is solely fuelled by the females' lipid reserves (Hirche et Niehoff 1996). The adaptive advantage for the offspring, hatched ahead of the phytoplankton bloom and slowly developing on endogenous reserves to first-feeding stage, is that they are ready beforehand to fully exploit the intense but brief summer season of biological production (Conover et Huntley 1991). Within a few weeks, strong grazing on microalgal cells enables them to rapidly grow and recruit to copepodites large enough to overwinter (CIII-adults). In preparation for diapause and reproduction, this copepod is the most efficient at storing lipids, mostly as wax esters, in oil sacs exceeding 65% of dry mass (Pasternak et al. 2001; Falk-Petersen et al. 2009). Over its vast geographical range, *C. hyperboreus* can modulate its generation time between 1 and at least 4 years depending on prevailing environmental conditions (Hirche 1997).

To model the response of this key copepod to the rapid climate-driven changes in the Arctic sea-ice regime, important traits of its life history need to be better documented, particularly for the winter months when reproduction occurs. In this study, we provide a detailed description of the reproduction cycle and population dynamics of *C. hyperboreus*, based on a quasi-annual time series during a period of record low ice cover in the southeastern Beaufort Sea (October 2007-July 2008). We addressed the hypothesis presented by Ringuette et al. (2002) that a lengthening of the ice-free season on Arctic shelves will promote population growth of large herbivore copepods such as *C. hyperboreus.*

3.4. Material and methods

2.6.4 Study area

The Amundsen Gulf, bounded by Franklin and Darnley bays to the south and Banks Island to the north, bridges the Beaufort Sea and eastern Mackenzie Shelf with the Canadian Arctic Archipelago (Figure 2.1). This large channel (~60000 km^2) is characterized by a small central basin, with a maximum depth close to 600 m between the southern tip of Banks Island and shallow Darnley Bay. Three main water masses lie in the region: the Polar-Mixed Layer (PML ; salinity <31.6; 0–50 m), the Pacific Halocline (PH ; $32.4 < S < 33.1$; 50–200 m), and the warmer Atlantic Waters (AW ; S >34; >200 m) (Carmack et Macdonald 2002). The generally weak surface circulation is dominated by the anticyclonic Beaufort Gyre that carries the pack ice and surface waters westward toward the Canada Basin (Carmack et Macdonald 2002; Ingram et al. 2008). This exchange between the Beaufort Sea and Amundsen Gulf is subject to large inter-annual variability (Barber et al. 2010). Below ∼80 m depth, the Beaufort shelf-break jet transports waters of both Pacific and Atlantic origin along the continental slope and into Amundsen Gulf (Carmack et Macdonald 2002; Pickart 2004). Within the gulf, deep circulation is usually weak and highly variable (Ingram et al. 2008). Sea-ice starts to form in October at the coastal margins of the gulf and consolidation over the entire area is completed by December (Galley et al. 2008). Ice breakup usually begins in late May-early June (1979-2000 average) and the section of the flaw lead polynya at the mouth of the gulf enlarges to form the Cape Bathurst Polynya complex (Barber et Hanesiak 2004). Remote sensing revealed considerable inter-annual variability in the extent and persistence of open water (Arrigo et van Dijken 2004).

2.6.5 Sampling

Zooplankton samples were collected between 16 October 2007 and 30 July 2008 at 78 stations in the southeastern Beaufort Sea during the International Polar Year expedition of the research icebreaker CCGS Amundsen (Figure 2.1). Most of these stations (66) were sampled in western Amundsen Gulf and the 12 remaining were located on the Mackenzie outer shelf and slope, Darnley and Franklin bays, and along the northwest coast of Banks Island as far north as McClure Strait, thanks to the record low ice concentration in June and until July 2008 in this sector of the Beaufort Sea (Barber et al. 2010). Sampling for egg production experiments and carbon-content analysis on *Calanus hyperboreus* had also been carried out during a previous overwintering program, the Canadian Arctic Shelf Exchange Study (CASES) project, in neighboring Franklin Bay from October 2003 to May 2004.

Sampling procedures pertaining to zooplankton in 2007-2008 as well as the characterization of environmental variables (sea-ice, temperature, salinity and pelagic chlorophyll a (chl *a*)) are detailed in Darnis and Fortier (2012). Data on ice-algae concentration were obtained from the study of Wold et al. (2011), also providing details on the ice-algae sampling. Briefly, prior to net sampling, the deployment of the rosette sampler fitted with a SBE911 plus® CTD and a Seapoint® fluorometer provided profiles of salinity, temperature and in situ fluorescence. The latter were calibrated using chl *a* concentrations determined for water samples taken at discrete depths.

Depth-stratified samples for the assessment of zooplankton abundance were acquired by deploying a 0.50-m^2 square aperture Hydrobios® multinet sampler carrying nine nets of 200 µm mesh size each fitted with a 2-L rigid codend. The sampler was hauled vertically from 10 m above the seafloor to the surface at a speed of 0.5 m s^{-1}. Three 20-m depth layers were sampled from 10 m off the bottom upward, and three from 60 m depth to the surface. The inconstant interval between 70 m above the seafloor and 60 m depth was divided in three equal sampling layers, the thickness of which was function of station depth. Upon retrieval, the samples were split in halves using a Motoda splitting box. One half from each sample was preserved in a borax-buffered seawater solution of 4% formaldehyde for taxonomic identification.

In both years (2003-2004 and 2007-2008), live zooplankton for the egg production experiments and biomass were captured using a 1-m^2 square aperture vertical sampler with a 200-µm mesh net and a 2-L rigid codend with filtration apertures located at the top of the cylinder. The sampler, lowered codend-first to avoid filtering on the way down, was towed vertically from 10 m above the bottom to the surface at 0.5 m s^{-1}. Upon recovery, the plankton catch was diluted in 0^{o}C-filtered seawater and cnidarians were immediately removed to reduce zooplankton mortality. The sample was kept at 0^{o}C until the *Calanus hyperboreus* copepodites were sorted in the laboratory. Attached to the main sampler, a 50 µm mesh 1-m long net of 81 cm^2 mouth aperture sampled eggs and nauplii of *Calanus* spp. The samples were preserved in a borax-buffered 4% formaldehyde solution.

2.6.6 Taxonomic and biomass analyses

In the laboratory, the formalin-preserved samples were rinsed and size fractionated on a 1000-µm sieve before re-suspension in distilled water. Known aliquots were taken from the 200-1000 and >1000-µm size fractions using a Henson-Stempel pipette and a Motoda splitting box, respectively, to collect from each fraction approximately 300 copepods that were enumerated, measured and identified to species, or to the lowest taxonomic level attainable. Young copepodite stages (CI-CIII) of *C. hyperboreus* and its congener *C. glacialis* were differentiated based on specific prosome lengths which differences were established during the Canadian Arctic Shelf Exchange Study (CASES) 2003-2004 expedition in the southeastern Beaufort Sea (Forest et al. 2011a). The highly similar eggs and naupliar stages of the two *Calanus* species were not differentiated.

Carbon content of the copepodite stages was estimated using one prosome length-C relationship established for the spring period ($C = 6.401PL^{2.966}$), and another for summer-winter ($C = 7.258PL^{3.074}$) (Forest et al. 2011a). Furthermore, the females incubated for the EP experiments were carefully blotted with absorbing material and preserved individually in cryovials at -20°C. On land, at least 10 of them were transferred to pre-weighed tin cups and oven-dried at 60°C for 48 h before dry weight (DW) measurement on a Sartorius ME5® microbalance (precision ± 1 µg). A number of these tin cups were burned at 925°C in a Perkin Elmer CHN 2400 Series II Elemental Analyzer (accuracy, 0.3% and precision, 0.2%) to measure the C content of the female copepods. An appropriate C:DW ratio was used to transform the other DW measurements to carbon content.

2.6.7 Egg production

Rapidly after capture, females in good condition were selected under a stereomicroscope and gently sorted from the plankton live catch by use of a truncated pipette. The procedure was carried out in dim light while the animals were at all times maintained at a temperature close to the conditions in situ (0-0.5°C). Thirty of the randomly sorted females were individually placed in 45-mL petri dishes, filled with 0.7-µm filtered seawater, and fitted with a false bottom (333-µm mesh) to prevent egg cannibalism. After incubation at 0°C for 24 h in the dark, eggs were counted and the conditions of the females verified prior to their preservation at -20°C for future DW and C measurements. As most of the spawning occurred in the evening hours, with many of the shed eggs floating, verification for spawning was increased at this particular time to limit cannibalism on the eggs not protected by the false bottom.

3.5. Results

3.5.1 Sea ice and chlorophyll

In late October, the ice cover was rapidly forming when zooplankton sampling started in Amundsen Gulf, and its consolidation was completed by December (Figure 3.1). By mid-March, ice-algae mats started to build-up rapidly in the lowermost 3 cm of the ice and reached their thickest layers (20 mg chl *a* m^{-2}) between mid-April and early May, after which the rapid ice-break-up prevented any further ice-algae development. The quick ice-cover decline, that started one month earlier than the average, cleared Amundsen Gulf of most of its ice by early July (<5% ice concentration). In late October 2007, chl *a* concentrations, averaged over the 0-80 m surface layer, nearly reached 1 µg L^{-1}; but the rapid decline of photosynthetically active radiations and extension of ice cover drove fluorescence close to nil values from November to the first records in late April 2008 of concentrations above 0.1 µg L^{-1} under the ice. A first microalgal bloom (chl *a* >1.5 µg L^{-1}) was recorded in mid-May in the central Amundsen Gulf once the ice cover went below the 50% threshold. Following this high primary production event, a period of relatively low fluorescence (<0.5 µg chl *a* L^{-1}) in the 0-80 m layer lasted the entire month of June before the development of strong subsurface chl *a* maximum in July.

3.5.2 Abundance, biomass and ontogenesis in the southeastern Beaufort Sea

Over the 2007-2008 quasi-annual cycle in the southeastern Beaufort Sea, integrated abundance of *Calanus hyperboreus* copepodites ranged from 398 to 15,265 ind. m^{-2}, with no apparent seasonal pattern (Figure 3.2a), and averaged 2,237 ± 2,015 ind. m^{-2}. The highest total abundance, by far, occurred in mid-April at a 520 m depth site in the central basin of Amundsen Gulf. This deep area (depth range 350-630 m) repeatedly yielded the highest abundances of this species during the overwintering season, as illustrated by the peaks from October to April (average 4,393 ± 3,154 ind. m^{-2}, n = 15). The two peaks >6,000 ind. m^{-2} in late May and early July were recorded at relatively deep stations (>350 m) off the northwest coast of Banks Island (Station 60 in Figure 3.1) and in McClure Strait (Station 71). At the two sites, high numbers of CI in May, and CII in July, were responsible for these peaks in abundance. Positive correlations were found between bottom depth and abundances of CIV (Spearman $r_s = 0.36$, $p = 0.001$), CV ($r_s = 0.66$, $p < 0.0001$), adult males (AM) ($r_s = 0.33$, $p = 0.0032$), and adult females (AF) ($r_s = 0.57$, $p < 0.0001$), whereas abundances of the younger stages were not correlated with this variable.

From October to April, the main overwintering stages were CIV (41%), adult females (AF) (34%), and to a lesser extent CV (13%) and CIII (8%) (Figure 3.2b). These stages were present year-round in Amundsen Gulf, but their contributions to the population showed different seasonal fluctuations. The relative importance of CV declined throughout the overwintering season until late April and then increased steeply in May and early June at the time when CIV contribution was decreasing quickly. After the June lowest contributions (1-6 %), recruitment of CIV in the population of *C. hyperboreus* resumed in July. The variable AF share reached its maximum, close to 50% of the population, during the month of March. The contribution of this adult stage was always above 20%, except in late May when sampling was carried out off the western coast of Banks Island, and in late June-early July. Adult males (AM) were present in low numbers only from late October 2007 to early June 2008, with an average contribution of 3% of the copepodites, and male:female ratios >0.2 were only found from 28 October to 21 January. In Amundsen Gulf, the first significant cohort of CI (13% of the population) appeared on 22 May, but massive (>75%) recruitment of CI was only observed on 26 and 27 May off the western coast of Banks Island (Stations 59 and 60; Figure 2.1) and this stage never dominated in Amundsen Gulf. About one month later, stages CII dominated the population only at two shallow sites (~200m) at the periphery of Amundsen Gulf (stations 65 and 66 near Cape Bathurst and the southwest coast of Banks Island, respectively) and in McClure Strait. By mid-July young stages CI-CII were found no more.

Following closely the pattern described for abundance, spatial variability was more strongly expressed in the integrated *C. hyperboreus* biomass than seasonal change (Figure 3.2c). Biomass ranged from 0.53 to 12.5 g C m^{-2} over the 10-month time series in the southeastern Beaufort Sea, and averaged 2.3 ± 1.7 g C m^{-2}. Most of the highest biomass values (>4 g C m^{-2}) were recorded at stations in the deep central Amundsen Gulf during the overwintering period (Figure 2.1 and 3.2c). Using the dataset for the whole study region, bottom depth and population biomass were positively correlated (Spearman $r_s = 0.65$, $p < 0.0001$). During the entire study period, AF largely dominated the *C. hyperboreus* biomass, with 67% of the share (Figure 3.2d), followed by CV (15%) and CIV (12%), leaving AM and young stages CI-CIII to account for the remaining 6% of total biomass.

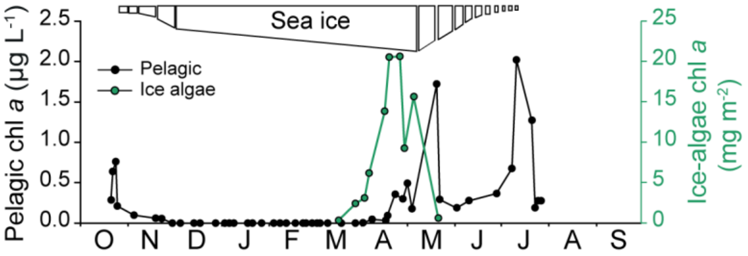


Figure 3.1. Time series of ice algae and pelagic chl *a* concentration averaged over the 0-80 m surface layer from October 2007 to July 2008 in Amundsen Gulf.

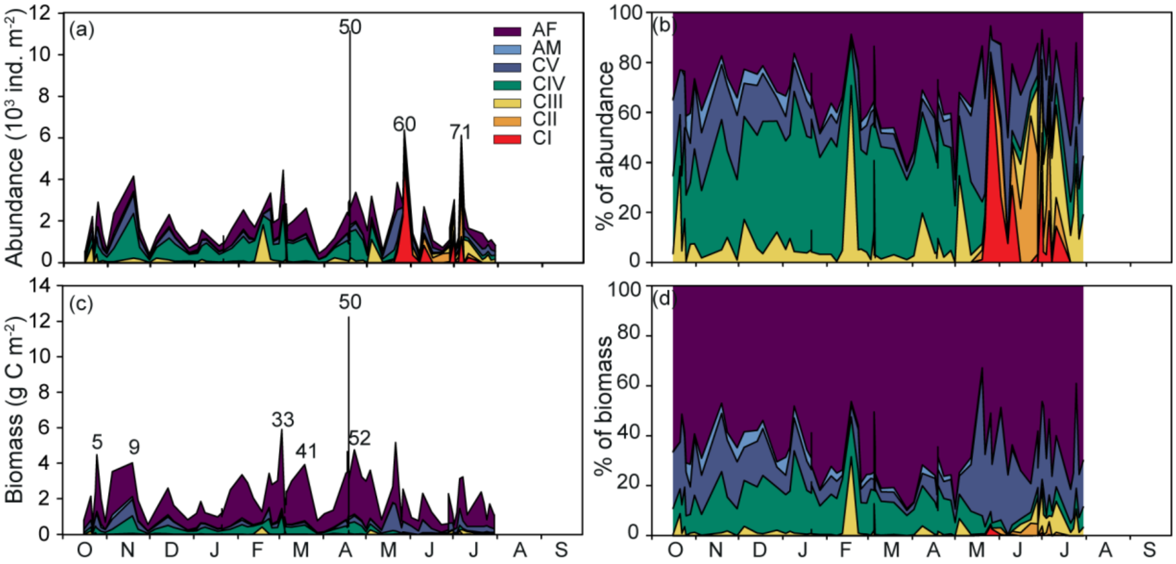


Figure 3.2. *Calanus hyperboreus*. Seasonal change in abundance (a), numerical composition (b), biomass (c), and composition in terms of biomass (d) from October 2007 to July 2008 in southeastern Beaufort Sea. Numbers in 2a and 2c refer to station identification in Figure 3.1.

3.5.3 Vertical distribution

The overwintering stages CIII-CV and AF showed all a pronounced pattern of seasonal ontogenetic migration (Figure 3.3a-c and e) with a deep distribution from October to April-early May, a period representing much of the long overwintering season. Adult males were essentially found at depth during this time. Stages CIII and AF were the first to congregate to the surface layer in late April (Figure 3.3a and e) and their ascent coincided with the decline in ice algae and the first occurrence of measurable chl *a* in the surface layer, most likely due to ice algae sloughed off their ice matrix (Figure 3.1). The ascent of CIV and CV followed shortly in early May (Figure 3.3b and c) and all the stages were in the surface layer for the onset of the early phytoplankton bloom that occurred at ice break-up. After spending May and June in the upper water column, AF initiated their downward migration (Figure 3.3e) before the second peak in pelagic primary production occurred in July. In late July, most of the CIII to CV were still distributed in the surface 0-100 m of the water column, but deeper than during the previous spring-summer period as they seemed to avoid the 0-40 m layer.

3.5.4 Reproduction in Amundsen Gulf

In Amundsen Gulf, the season of reproduction of *Calanus hyperboreus* extended from mid-January to mid-April (Figure 3.4) while the females were at depth and before any sizeable chl *a* concentrations could me measured in the surface water column in 2008. A similar timing of reproduction was found in Franklin Bay, as the first spawning female laid a small clutch (26 eggs) in late December 2003, and the last in late April 2004 (Figure 3.4a). However, the egg production rates were higher in 2008 (31 ± 17 eggs f^{-1} d^{-1}, averaged over the reproduction season) than in 2004 (14 ± 10 eggs f^{-1} d^{-1}). Despite the apparent lack of dependence of reproduction on a food source, daily egg production rates were highly variable in 2008, ranging between 7 and 65 eggs f^{-1} d^{-1}, or 20-65 eggs f^{-1} d^{-1} when just the peak February-March production period is considered (Figure 3.4a). Strong variability was also seen in the clutch size, for most of the experiments, but also throughout the season (Figure 3.4b). Clutch size ranged between 65 and 194 eggs $clutch^{-1}$ without any obvious temporal pattern, and the maximum clutch of 404 eggs was counted in late February. At the start of reproduction in mid-January, the proportion of spawning females increased steeply, from 3% to 33%, in a two-week time (Figure 3.4c). A swift decrease in the spawning frequency occurred in late March at the end of the reproduction season, right after the record 40% of spawning females in the population was measured. The mean spawning frequency during the February-March high reproduction period was 28 ± 6 % of the total females.

Total daily egg production by the population of females (individual egg production rate x density of females) increased rapidly from 0 in late January to 35,848 ± 12,868 eggs m^{-2} d^{-1} in early February (Figure 3.5a) and remained high but variable (mean 28,706 ± 14,223 eggs m^{-2} d^{-1}) throughout the February-March period of intense individual egg production rates, before a steep decrease occurred from mid-March to early April. Because of equivocal species identification of eggs and nauplii between *Calanus hyperboreus* and its congener species *C. glacialis*, these were pooled in a single *Calanus* spp. group from April onward, and from October to December (Figure 3.5b). These assumptions were based on the knowledge, provided by egg production experiments, that *C. glacialis* initiated its reproduction in early April (data not shown) and *C. hyperboreus*, in January.

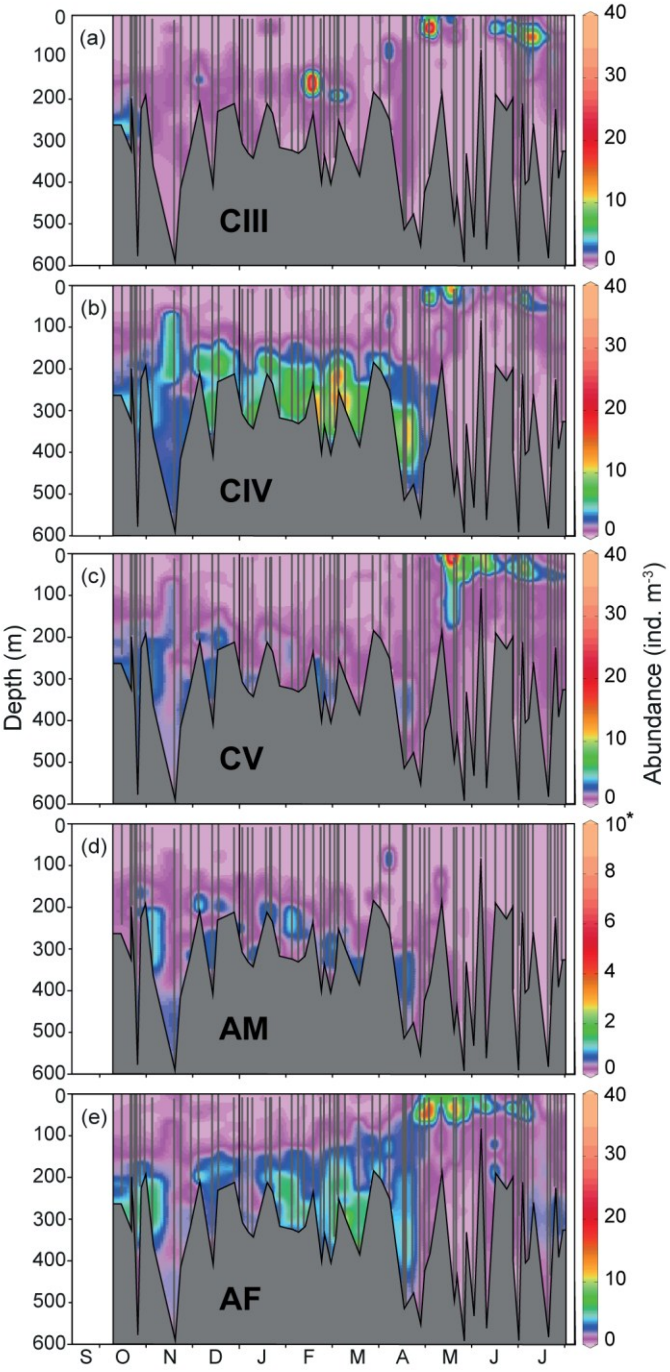


Figure 3.3. *Calanus hyperboreus*. Time-depth section of abundance of the overwintering stages CIII-adults along the track of the ship in southeastern Beaufort Sea from October 2007 to July 2008. Vertical lines indicate sampling dates. Note the change of scale for the adult males (AM).

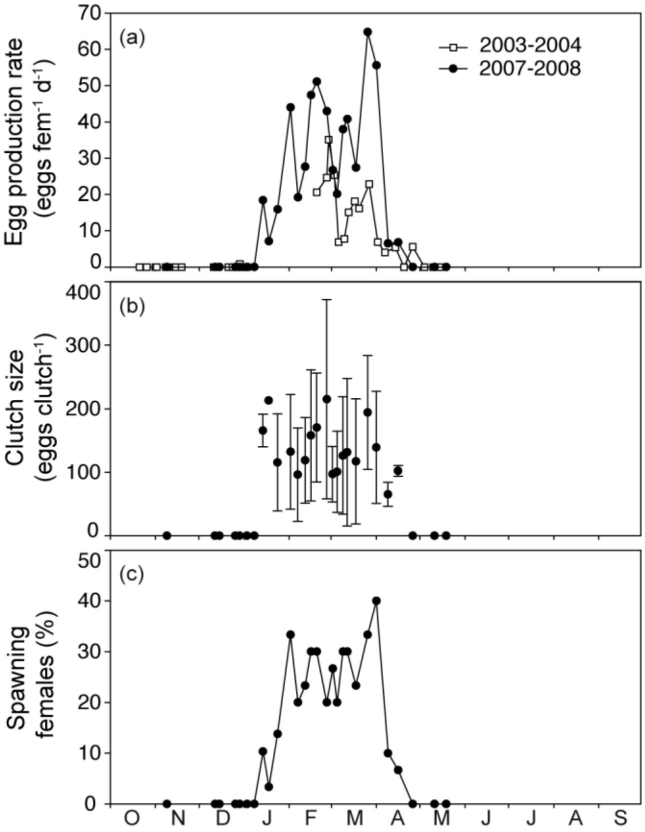


Figure 3.4. *Calanus hyperboreus*. Time series of egg production rate (EPR) in Amundsen Gulf in 2007-2008 and Franklin Bay in 2003-2004 (a), clutch size (± 1 standard deviation) (b), and proportion of spawning females (c). The EPR experiments in 2003-2004 were run at an overwintering site (70°04'N, 126°26'W) in Franklin Bay and followed exactly the same procedures as in 2007-2008.

As expected, a period of high abundance of *C. hyperboreus* eggs coincided with the peak reproduction phase, namely February-March during which an average 28,863 ± 23,310 eggs m^{-2} were distributed in the water column of Amundsen Gulf and a peak of 106,952 eggs m^{-2} was recorded on 20 February (Figures 3.4a and 3.5b). Nauplii of this species became most abundant in early March, peaking at 55,386 ind. m^{-2} on 12 March, and were composed essentially of stages NI to NIII (Figure 3.5c). Their abundance decreased dramatically to <6,000 ind. m^{-2} in mid-April, indicating that a large fraction of the numerous eggs spawned in mid-March were not developing into early naupliar stages. The first NIV appeared in mid-April and was most probably *C. hyperboreus*, but from then on the *Calanus* nauplii might have been a mix of the two *Calanus* species.

3.5.5 Seasonal variability of adult females carbon content

From October 2007 to the end of February 2008, the individual carbon content of adult females showed no particular trend and averaged 2.9 ± 0.42 mg C (Figure 3.6). But by early March, in the middle of their reproduction season, the mass of females had decreased considerably and this decline continued until mid-April, when the lowest carbon content of 1.34 ± 0.42 mg C f^{-1} was recorded. At the onset of the phytoplankton bloom in May, carbon content of females started to increase and, within three months, reached values in excess of 3.75 ± 0.59 mg C, representing a 2.8-fold increase from the April lowest values. In 2003 in Franklin Bay, the carbon content of adult females averaged 2.44 ± 0.41 mg C and was not statistically different from the mean carbon content measured in 2007, most likely because of the large variability in the body condition of females at any given site (Figure 3.6). Low-carbon females (1.33 ± 0.61 mg C) were already found in early March, although earlier occurrence of females with poor body condition cannot be excluded since there is a gap in the dataset extending from early January 2004 to early March 2004. Light females were still found in mid-May under the land-fast ice of Franklin Bay. Then, their carbon content more than doubled within two months to reach 2.75 ± 1.25 mg C, but this maximum value was significantly smaller than the one measured in 2008 at approximately the same date (t-test; $p < 0{,}0037$). In July and September, females' carbon contents were highly variable.

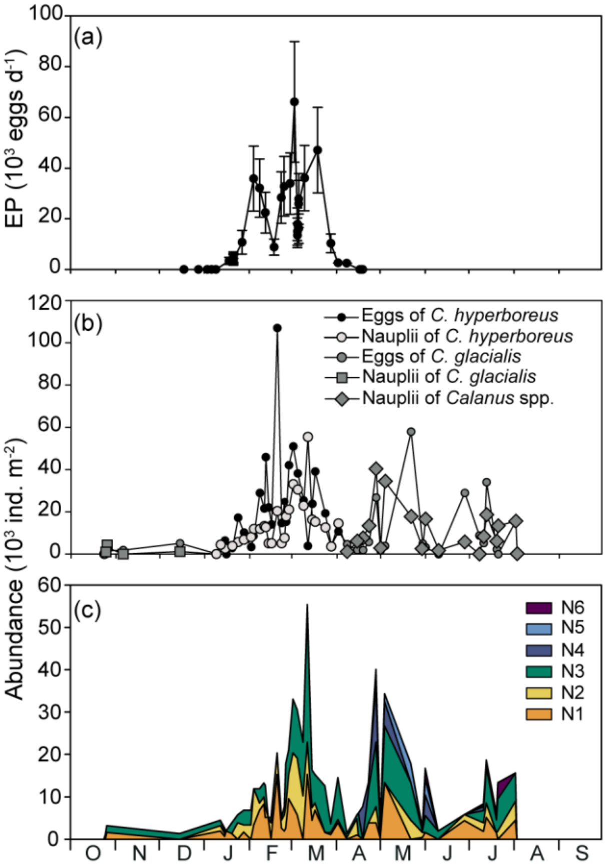


Figure 3.5. Time series of *Calanus hyperboreus* total egg production rates (a), water column total abundance of eggs and nauplii of *C. glacialis, C. hyperboreus* and *Calanus* spp. at stations >250 m depth within Amundsen Gulf (b), and abundance of each nauplius stage (c).

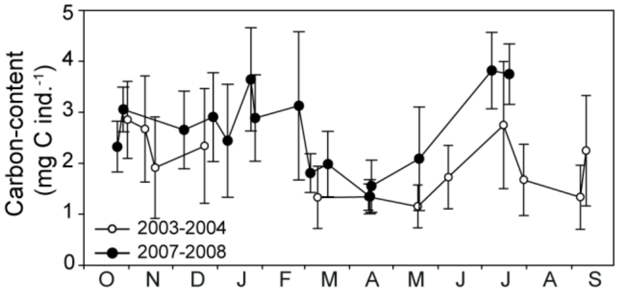


Figure 3.6. *Calanus hyperboreus*. Time series of individual carbon-content (± 1 standard deviation) of adult females captured in Amundsen Gulf in 2007-2008 and in Franklin Bay in 2003-2004.

3.6. Discussion

Previous studies have suggested that the lengthening of the growth season, induced by sea-ice earlier melting and later formation, will potentially lead to successful recruitment of key arctic copepod grazers such as *Calanus hyperboreus*, *C. glacialis* and *Pseudocalanus* sp., provided that sufficient pelagic primary production follows (Ringuette et al. 2002; Darnis et al. 2008; Forest et al. 2011a). On the other hand, shift in seasonality of ice-cover and primary production may increase the risk of mismatch between the supply of essential food resource and copepod life history traits like the occurrence of first-feeding developmental stages (Varpe et al. 2007). Following the record low sea-ice extent of autumn 2007 over the Amerasian Arctic Ocean (NSIDC 2010), the ice cover in Amundsen Gulf receded rapidly from early May onward, about one month earlier than usual (Galley et al. 2008). Furthermore, total gross primary production, estimated from nutrient drawdown over spring-summer 2008, was about 80% higher than estimates made during the CASES program at the same period in 2004 (Forest et al. 2011b), a year of average ice concentrations and less dynamic ice cover (Galley et al. 2008). With this context, the CFL 2007-2008 quasi-annual time series appears as a useful dataset to study how changes in the timing of primary production may affect recruitment in the population of *Calanus hyperboreus*, and influence some of its life history traits.

3.6.1 Life cycle of *Calanus hyperboreus* in the southeastern Beaufort Sea

In Amundsen Gulf, the overwintering *Calanus hyperboreus* population remained fairly stable throughout the period October-April during which it comprised predominantly copepodite stages CIV and adult females. The simultaneous presence of several overwintering stages is typically indicative of a multi-annual life cycle in arctic seas and in the northwest Atlantic (Conover 1988; Hirche 1997; Plourde et al. 2003). With CIV as the primary overwintering stage, we propose a 2- to 3-year life cycle for this species in Amundsen Gulf. This life cycle is in good agreement with those reported for areas characterized by a longer open-water season of biological production, such as the eastern North Water polynya (Ringuette et al. 2002), Disko Bay on the south-western Greenland coast (Madsen et al. 2001; Swalethorp et al. 2011), the Atlantic water of the Westspitsbergen Current (Hirche 1997), and the lower St-Lawrence Estuary further south (Plourde et al. 2003). There, the *C. hyperboreus* offspring hatch prior to the ice-algae and phytoplankton blooms, and seem to have time to achieve stage CIV in the first growth season. These CIV would develop into CV in the spring or summer of the second year, and adults would gradually recruit from stage CV from autumn onward (Conover 1988). Females may reproduce in their first winter if they have sufficient lipid reserves to do so, or may have to wait after another growth season to complete the cycle in their third year of life (Conover et Siferd 1993). On the other hand, a life cycle of at least three years was proposed, based on the dominance of stage CIII in the overwintering population, over the heavily ice-covered central Arctic Basin (Dawson 1978), Resolute Passage in the Canadian Arctic archipelago (Conover 1988), but also in the more ice-free Central Greenland Sea Gyre (Hirche 1997). Conover and Siferd (1993) suggested also a 3- to 4-year life cycle in Barrow Strait although CIV was the prevalent overwintering stage in the winters of 1984 and 1985. They doubted that this late developmental stage could be achieved in a single and usually short growth season (2.5 and 3 months in 1984 and 1985, respectively) in this sector of the Canadian Arctic archipelago. However, this was likely not the case in Amundsen Gulf in 2008 as the precocious onset of the ice break-up extended the potential growth season to >5 months and would have allowed the young *C. hyperboreus* to develop to stage CIV.

During 2008, cohort development was evident within the *Calanus hyperboreus* copepodite stages once the spring phytoplankton bloom signaled the onset of the season of pelagic primary production. Like Hirche (1997) suggested for the Greenland Sea, overwintering stages CIV took advantage of the high supply of diatoms in May (Forest et al. 2011b) to grow and rapidly molt into stages CV. But the capacity for fast accumulation of high-energy compounds is best illustrated with the case of the adult females. They were among the first to ascend to the surface in late April, approximately two weeks before the ice break-up and the intense first phytoplankton bloom. Within two months in the upper part of the water column, they nearly tripled their carbon content from the minimum values attained in mid-April (Figure 3.6), after either completing reproduction at depth or molting from CV. Again, adult females were the first stage to initiate the seasonal downward migration in early July while there was still relatively high pelagic primary production forming a strong sub-surface chlorophyll maximum (SCM). Significant development of CII into CIII and CIII into CIV started in mid-June and early July, respectively. As a strong pattern of downward migration was not seen for these stages in late July, in contrast to adult females, it is probable that they remained close to the SCM after the end of the study to feed on the diatom production. Thus, the stages CI and CII that first appeared in the surface layer in May were presumably capable of achieving development to stage CIV in 2008 before migrating to depth for the overwintering period, like the scenario of a 2- to 3-year life cycle implies for this species in the region.

The timing of copepodite recruitment in May (i.e. the appearance of the first stages CI in the population) and apparent match between new CI and high phytoplankton new production were similar to those reported for the eastern North Water polynya and Disko Bay, two regions that traditionally witness an earlier onset (by 1-2 months) of the phytoplankton bloom than the southeastern Beaufort Sea (Madsen et al. 2001; Ringuette et al. 2002). The relationship between the timing of the bloom and the timing of recruitment of CI, observed in Amundsen Gulf and in other sectors over the geographical range of *Calanus hyperboreus* (Ringuette et al. 2002), supports the assumption of a specific adaptation of the spawning strategy of this species to ensure that first-feeding naupliar stages appear with the onset of pelagic primary production (Conover et Huntley 1991). This approach should maximize growth, development to overwintering stages and lipid storage during a summer season of often brief but intense pelagic primary production.

3.6.2 Reproduction

Our two time-series of egg production rates, for 2003-2004 in Franklin Bay and 2007-2008 in Amundsen Gulf, enable to delimit the reproduction season of *Calanus hyperboreus* from mid-January to mid-April in the southeastern Beaufort Sea. The prime mating period would be from November to January when the male:female ratio reaches its highest (>0.2). Such timing of reproduction is fairly similar to those reported for the central Arctic Ocean (January-May) (Johnson 1963), Disko Bay (February-mid-April) (Niehoff et al. 2002) and the Lower St. Lawrence Estuary (January-late March) (Plourde et al. 2003). However, reproduction is delayed until between mid-March and May in the Canadian Arctic archipelago (Conover et Siferd 1993), and between May and June in Foxe Basin (Grainger 1965), two areas with typically late ice break-up. By contrast, in the central Greenland Sea characterized by a much more sporadic ice cover, reproduction ranges over a longer period covering November to late March/April (Hirche et Niehoff 1996). Nevertheless, in all cases the reproductive cycle was completed while the females were at depth, experiencing a fairly stable ambient temperature, and before any sizeable primary production could be measured in the surface layer. This corroborates the fact that *Calanus hyperboreus* females fuel their egg production solely with their lipid reserves (Hirche et Niehoff 1996). The reproduction strategy (timing and duration) of this species is thus independent of the *in situ* environmental setting, but most likely result from local adaptation and acclimatization to variability in food supply for the offspring, as well as body condition and physiology of the females in the preceding year (Conover et Siferd 1993; Hirche et Niehoff 1996; Varpe 2012).

So far, no published study has documented spawning variability over the entire winter reproductive season of *Calanus hyperboreus*, and only a few provide estimates of *in situ* egg production rates to compare our data with (Hirche et Niehoff 1996; Madsen et al. 2001; Henriksen et al. 2012). With females spawning individually 31 ± 17 eggs d^{-1} (mean ± 1 SD) over the whole reproduction season, egg production rates measured in Amundsen Gulf in 2008 are relatively high. They exceed those for February-March from the neighboring Franklin Bay in 2004 (19 ± 9 eggs f^{-1} d^{-1}) (Figure 3.4a) and

Greenland Sea (9 ± 9 eggs f^{-1} d^{-1}) (Hirche et Niehoff 1996), and are equivalent to the single estimate of 33 eggs f^{-1} d^{-1} made in Disko Bay in mid-March 1997 by Madsen et al. (2001). Furthermore, the range of egg production rates between February and early April 2008 (7-65 eggs f^{-1} d^{-1}) compares well with the one for the same period in Disko Bay in 2009 (4-54 eggs f^{-1} d^{-1}) (Henriksen et al. 2012). The higher individual egg production observed in Amundsen Gulf in 2008, compared with Franklin Bay in 2004, could reflect a better growth season for the stages CV and adult females in the early summer of 2007 than in 2003. However, lack of data on the body conditions of most of the 2004 spawning females precludes any substantiation of this speculation.

3.6.3 Control of recruitment

As reported earlier, recruitment of stages CI coincided with the onset of a strong phytoplankton bloom in May. However, these new CI only contributed 13% to the population abundance, suggesting that recruitment in Amundsen Gulf was modest compared to the sites off the western coast of Banks Island and in McClure strait (Figure 1), where CI represented >75% of the copepodites in late May. The fact that total abundance of *C. hyperboreus* did not increase from May to July further supports the assumption of poor copepodite recruitment in Amundsen Gulf in 2008 since this species had already terminated its reproduction by early April and no additional CI recruits could thus be expected after July. In February-March, high total egg production rates (8,829-66,824 eggs m^{-2} released daily by the population of females) and relatively high abundances of eggs (>28,000 ind. m^{-2}) and young nauplii NI-NIII (>17,000 ind. m^{-2}) in the water column indicated that *C. hyperboreus* had indeed a vigorous winter 2008 reproduction. Whether these eggs and nauplii suffered high levels of predation and/or the nauplii starved is an interesting but complex issue to investigate since the vertical distribution of both stages and the food of the nauplii are not well described.

Nauplius stage NV is likely the first feeding stage of *C. hyperboreus* according to Conover (1962) and Mauchline (1998). A rough approximation of the development time from spawning to NV as a function of temperature can be made using the Belehrádek's functions provided by Ji et al. (2012). Since most of the eggs and newly hatched nauplii are considered to float toward the near-freezing surface waters (Conover et Huntley 1991), they should experience temperatures ranging from around 0°C in the Atlantic layer to -1.7°C in the PML during the ascent. However, numerous non-feeding nauplii NI-NII were caught in sediment traps moored at 200 m depth in central Amundsen Gulf in winter 2004, indicating that the ascent may not necessarily be immediate (Ota et al. 2008). Applying the upper range of winter temperatures, it takes about 54 days for a *C. hyperboreus* egg to develop to NV at 0°C. Thus, eggs spawned at the end of February, right in the middle of the peak period of egg production, would have reached the first feeding stage in late April, when ice-algae stocks were at their maximum and chl *a* concentrations in the surface layer started again to be recorded, although at low levels (<0.5 µg L^{-1}). Late naupliar stages of calanids have been shown to sustain high growth rates at food concentrations low enough to be limiting to the late copepodite stages (Richardson et Verheye 1999; Hygum et al. 2000). Assuming that these feeding nauplii are mainly herbivores like the copepodites (Campbell et al. 2009; Forest et al. 2011a), they most likely were able to take advantage of diatom patches eroded from the ice at the peak of ice-algae production in April. The subsequent onset of ice-melt, which led a few weeks later to the break-up of ice cover and the simultaneous bloom, would also have provided favorable feeding conditions for the nauplii that hatched from eggs spawned throughout March. Thus, we surmise that the arrival of nauplii initiating feeding, and hatched from the large numbers of eggs spawned after February 2008, could match the availability of food (ice algae) at the under-ice surface or in the melt water layer just below (ice algae and phytoplankton). This was likely not the case for the nauplii NIII found in great numbers in late February-early March that may have fallen short of reaching the period of food availability, as they would have used their internal reserves to develop into first feeding stages sometime in the second half of March.

At least two observations support the hypothesis of a strong top-down control of the *C. hyperboreus* population at an early stage of its development. First, with a population egg production rate of 28,706 ± 14,223 eggs m^{-2} d^{-1}, averaged over February-March, and the knowledge that these eggs take at least nine days to develop to stage NI (Conover 1988; Ji et al. 2012), a much larger accumulation of eggs should be expected than the 28,863 ± 23,310 eggs m^{-2} recorded for the same period. In fact, no eggs appeared to accumulate, as their abundance was equivalent to the total number of eggs released daily. The large deficit of eggs measured in the water column relative to the production and development time suggests the impact of predation. Second, these substantial numbers of eggs spawned throughout March did not translate into high numbers of young nauplii in late March and early April as soon as reproduction lessened, indicating that they likely suffered high mortality by predation. Interestingly, the steep increase in the respiration per unit mass of the mesozooplankton size fraction >1000 µm, in mid-March at depth (Darnis et Fortier 2012), corresponded to high discharge of *C. hyperboreus* eggs in the deep water column and declining abundance of eggs and nauplii, but also to a time of especially low sympagic primary production in the inner surface of the ice. Thus, the carbon supplied by these lipid-rich eggs to the environment in winter should represent a crucial food resource for mesozooplankton omnivores and carnivores, such as *Metridia longa*, *Aetideopsis* spp., *Gaetanus* spp., *Gaidius* spp. and *Paraeuchaeta glacialis*, at a time of otherwise poor biological production.

In particular, the mesopelagic copepod *M. longa* must have played a chief role in the top-down control of recruitment of *C. hyperboreus* in the Amundsen Gulf in 2008. Late developmental stages of *M. longa* are known predators of the orange-colored eggs and nauplii of *C. hyperboreus*, as shown by a change in color of their guts occurring at the peak of egg production of *C. hyperboreus* in March (Conover et Huntley 1991; Darnis et al. 2012). This egg consumption likely triggered a first reproduction event by females of *M. longa* in late March (G. Darnis; unpublished data). Feeding experiments run in the northwest Atlantic showed that members of the genus *Metridia* could ingest eggs of *Calanus* spp. at rates as high as 34 ± 9 eggs ind.$^{-1}$ d^{-1} (Sell et al. 2001). With a vertical distribution at midwater depth, above the *C. hyperboreus* spawning females, stages CV and adults of *M. longa* were strategically positioned to intercept the numerous *Calanus* eggs and nauplii floating toward the under-ice surface in February-March (Chapter 2). Plourde et al. (2003) reported a negative relationship between the abundances of these two species over several years (1979-1980 to the late 1990s) in the lower St. Lawrence Estuary, where a decline in *C. hyperboreus* population had been accompanied by a 10-fold increase in abundance of *M. longa*. With a mean integrated abundance of 16,193 ± 13,068 ind. m^{-2} over 2007-2008 (Darnis et Fortier 2012), the population size of *M. longa* in Amundsen Gulf was large by arctic standards. It was >2 times higher than the mean abundance in the same area in autumn 2002 (5,907 ind. m^{-2}) (Figure 3.8; Darnis et al. 2008), in neighboring Franklin Bay in 2003-2004 (7,894 ± 3,782 ind. m^{-2}) (Forest et al. 2008), and at the sites >200 m depth outside the gulf in 2008 (4,917 ± 1,988 ind. m^{-2}) (Figure 3.7). In the biologically productive eastern North Water polynya in spring-summer 1998, *M. longa* were also less abundant (8,990 ind. m^{-2}) (Ringuette et al. 2002) than in the Amundsen Gulf in 2008 (Figure 3.7). By contrast, the integrated abundance of *C. hyperboreus* did not differ significantly between the different areas of the southeastern Beaufort Sea in 2007-2008 or in 2003-2004, or if the two annual cycles were compared (2,015 ± 1,573 ind. m^{-2} in 2007-2008 vs. 2,239 ± 2,321 ind. m^{-2} in 2003-2004). Therefore, a much-reduced *C. hyperboreus*/*M. longa* abundance ratio in the Amundsen Gulf in 2008, relative to other regions and years, underlines the potential for stronger predation pressure of the omnivore *M. longa* on the eggs and offspring of the herbivore *C. hyperboreus* during this study.

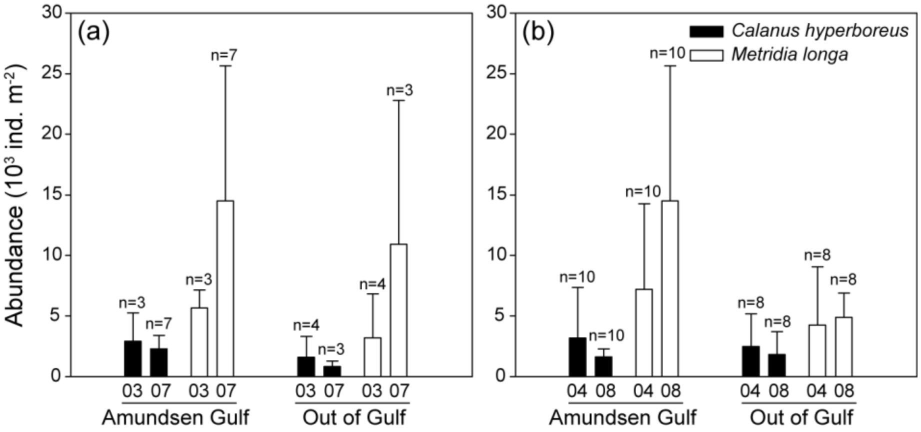


Figure 3.7. Inter-annual comparisons of integrated abundances of *Calanus hyperboreus* and *Metridia longa* in the Amundsen Gulf and at sites >200-m depth outside of the Gulf for 2007 vs. 2003 during autumn (10 October-19 November) (a) and 2008 vs. 2004 during summer (13 June-31 July) (b).

3.7. Conclusion

Tremblay et al. (2011) revealed that reduced sea-ice cover along with upwelling favorable atmospheric conditions boosted several-fold the production of ice algae, phytoplankton and of the key shelf species *Calanus glacialis* over the coastal Beaufort Sea in autumn 2007 and summer 2008, in comparison with respective periods in 2003 and 2004. By contrast, our analysis of the dynamics and stock of *Calanus hyperboreus* in the deeper Amundsen Gulf fails to identify strong recruitment and population growth for this oceanic *Calanus* species in 2008 despite an 80% increase in total primary production compared to 2004 (Forest et al. 2011b). The short time-lag of 1-3 months between a 2008 vigorous winter spawning and the onset of the ice-algae bloom and precocious phytoplankton production refutes the scenario of a mismatch between the bulk of the first-feeding developmental stages and food availability to explain this rather poor recruitment. Population development, obviously, is not severely limited by environmental conditions in the southeastern Beaufort Sea since *C. hyperboreus* can condense its life cycle to a 2 to 3-year duration there, just as in other arctic regions like the North Water polynya and Disko Bay, traditionally experiencing early onset of extensive biological production (Madsen et al. 2001; Ringuette et al. 2002). On the other hand, the copepod *Metridia longa*, the third player in terms of abundance as well as biomass in 2007-2008 in the gulf (Chapter 4, Table 3.1), increased considerably its production in response to the relaxation of the ice regime and resulting favorable feeding conditions until late autumn 2007 (Figure 3.7a). We suspect that this abundant omnivore contributes largely to restrain population growth of *C. hyperboreus* by preying on its youngest stages during winter when other food sources in the system are scarce (Conover et Huntley 1991). With the ongoing lengthening of the ice-free season due to climate change, a thriving stock of *M. longa* could well intensify the top-down control of the recruitment of the herbivore *C. hyperboreus*, possibly to the extent of counteracting any potential benefits of increased pelagic primary production over the margins of the arctic shelves.

4. Chapitre 4 – Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean)

4.1. Résumé

Dans les mers arctiques, les lipides que les migrateurs zooplanctoniques accumulent dans la couche de surface au printemps et en été sont respirés en profondeur en hiver. Le transport actif en profondeur ainsi induit par les fractions de taille du zooplancton de 200-1000 et >1000 µm a été quantifié sur la base de 41 profiles de biomasse et de respiration d'octobre 2007 à juillet 2008 dans le Golfe d'Amundsen (Océan Arctique canadien). La petite fraction, dominée par les *Calanus glacialis* CII-CIII, a représenté en moyenne 12% de la biomasse zooplanctonique totale et a peu contribué au transport actif de carbone par la respiration. D'avril à juillet, le zooplancton total a ingéré 17-28% de la production primaire brute (PPB) dans les 100 m de surface, et 36-59% de la PPB sur l'ensemble de la colonne d'eau. La grande fraction, comprenant principalement les *Calanus hyperboreus et C. glacialis* CIV, CV et adultes qui accumulent d'importantes réserves lipidiques, était responsable de 89% du broutage. La migration en profondeur du grand zooplancton à la fin de l'été a coïncidé avec la forte diminution des taux de respiration spécifique signalant le début de la diapause et de l'alimentation endogène du métabolisme. D'octobre à avril, la respiration-migration de *Calanus* a transporté activement 3.1 g C m^{-2} au delà de 100 m, un flux représentant de 85 à 132% des flux gravitationnels de carbone organique particulaire à 100 m d'octobre à juillet. Nos résultats soulignent l'importance d'inclure le transport actif dû aux migrateurs du grand zooplancton dans les bilans de carbone de l'Océan Arctique.

4.2. Abstract

In arctic seas, lipids accumulated by zooplankton migrants in the surface layer in spring-summer are respired at depth during the winter. The resulting active downward transport of carbon by the 200-1000 and >1000 µm mesozooplankton fractions was quantified based on 41 biomass and respiration profiles from October 2007 to July 2008 in the Amundsen Gulf (Canadian Arctic Ocean). The small fraction, dominated by CII-CIII *Calanus glacialis*, represented on average 12% of the overall zooplankton biomass and contributed little to the active transport of carbon by respiration. From April to July, total zooplankton ingested 17-28% of the estimated gross primary production (GPP) in the surface 100 m, and 36-59% of GPP over the entire water column. The large fraction, comprised mainly of CIV, CV and adults *Calanus hyperboreus* and *C. glacialis* that accumulate large lipid reserves, was responsible for 89% of grazing. The downward migration of large zooplankton in late summer coincided with a sharp decline in specific respiration rates signalling the start of diapause and the endogenous fuelling of metabolism. From October to April, *Calanus* migration-respiration actively transported 3.1 g C m^{-2} beyond 100 m, a flux that represented 85 to 132% of the gravitational POC fluxes at 100 m from October to July. Our results stress the importance of including active transport by large zooplankton migrants in carbon budgets of the Arctic Ocean.

4.3. Introduction

In the ocean, several processes mediated by the zooplankton can either enhance or limit vertical carbon fluxes and, therefore, regulate the efficiency of the biological CO_2 pump (Hernández-León et Ikeda 2005; Tremblay et al. 2006; Kobari et al. 2008; Steinberg et al. 2008b). In the epipelagic layer of arctic seas in spring-summer, the large herbivorous copepods *Calanus hyperboreus* and *C. glacialis* exert heavy grazing pressure on the diatom-dominated phytoplankton bloom (Tremblay et al. 2006). Some of the assimilated photosynthetic carbon is immediately remineralized by respiration in the surface layer. But the energy stored in the large lipid reserves of *Calanus* will be respired later at depth, several hundred meters below the surface where the copepods overwinter for up to 10 months in a resting stage (Hirche 1997).

In the temperate and tropical ocean, the diel vertical migration (DVM) of the zooplankton is primarily responsible for this active export of carbon linked to respiration (Longhurst et Williams 1992). For instance, Hernández-León et al. (2001) calculated that the DVM respiratory flux SW of Gran Canaria and west of Tenerife represented 16-45% of the passive particulate export flux. By contrast, Longhurst and Williams (1992) concluded that the active transport of carbon to depth by the seasonal migration of zooplankton (mainly *Calanus finmarchicus*) was trivial relative to the gravitational flux of carbon. In arctic waters, the limited DVM of zooplankton (Blachowiak-Samolyk et al. 2006; Daase et al. 2008) likely contributes little to the downward respiratory flux. Previous studies suggest instead that the seasonal migration of large herbivorous copepods such as *Calanus hyperboreus* and *C. glacialis* could generate a significant downward respiratory flux by exporting to depth the lipids accumulated in spring-summer (Hirche 1997; Auel et al. 2003).

Small omnivorous and detritivorous copepods that numerically dominate arctic zooplankton are not known to undergo extensive ontogenetic vertical migrations (e.g. Fortier et al. 2001). Given their high turnover rates, continuous activity, and capacity to graze small particles, small copepods may contribute substantially to recycling organic carbon in the surface layer and to the attenuation of the vertical particulate organic carbon (POC) flux (Hopcroft et al. 2005). As opportunistic feeders that accumulate little if any lipid reserves, small arctic zooplankton, in particular copepods, are believed to remain active under the ice in the winter months (Sampei et al. 2009b). For instance, the predominance of small faecal pellets in the vertical POC flux in fall and winter (Forest et al. 2008; Lalande et al. 2009b) suggests that, as large herbivorous copepods migrate to depth to overwinter, these small copepods become, together with microzooplankton, the main grazers in the surface layer from the end of summer to the onset of microalgal production in spring/summer (Svensen et al. 2011).

The role of zooplankton grazing and respiration in mediating the vertical transport of carbon remains poorly resolved for Arctic waters, particularly for the winter months. During the international Circumpolar Flaw Lead system study (CFL), the research icebreaker CCGS *Amundsen* overwintered in the southeastern Beaufort Sea, remaining mobile in the flaw lead that separates the drifting central pack and the landfast ice. The 10-month expedition provided an unprecedented opportunity to monitor zooplankton biomass and respiration from October 2007 to July 2008 in the Amundsen Gulf. In this study, we track the vertical migration of the 200-1000 µm and >1000 µm zooplankton size fractions from October 2007 to July 2008. In particular, we measure the transport and remineralisation at depth of carbon that result from the annual vertical migration of the mesozooplankton, and assess its importance relative to other vertical carbon fluxes.

4.4. Material and methods

4.4.1 Study area and oceanographic setting

The Amundsen Gulf (60000 km^2) connects the Beaufort Sea and Mackenzie Shelf to the Canadian Arctic Archipelago (Figure 4.1). The western sector of the Gulf is bounded by Franklin and Darnley bays to the south and Banks Island to the north. The maximum depth of 600 m occurs in a small central basin between the southern tip of Banks Island and Darnley Bay. Water masses in the region comprise the Polar-Mixed Layer (salinity<31.6; 0–50 m), the Pacific Halocline (32.4<S<33.1; 50–200 m), and the warmer Atlantic Waters (S>34; >200 m) (Carmack et Macdonald 2002). The surface circulation is dominated by the anticyclonic Beaufort Gyre that entrains the pack ice and surface waters westward toward the Canada Basin (Carmack et Macdonald 2002; Ingram et al. 2008). Large inter-annual variability occurs in this exchange between the Beaufort Sea and Amundsen Gulf (Barber et al. 2010). Below ~80 m depth, the Beaufort shelf-break jet carries water of Pacific origin along the continental margin and into Amundsen Gulf (Carmack et Macdonald 2002; Pickart 2004). The deep circulation (>200 m) is weak and highly variable (Ingram et al. 2008). Sea-ice starts to form in October at the coastal boundaries of the gulf and consolidation is completed by December (Galley et al. 2008). By May-June, breakup begins and the flaw lead polynya enlarges to form the Cape Bathurst Polynya complex at the entrance of Amundsen Gulf. Satellite data indicate large inter-annual variability in the extent and persistence of open water (Arrigo et van Dijken 2004).

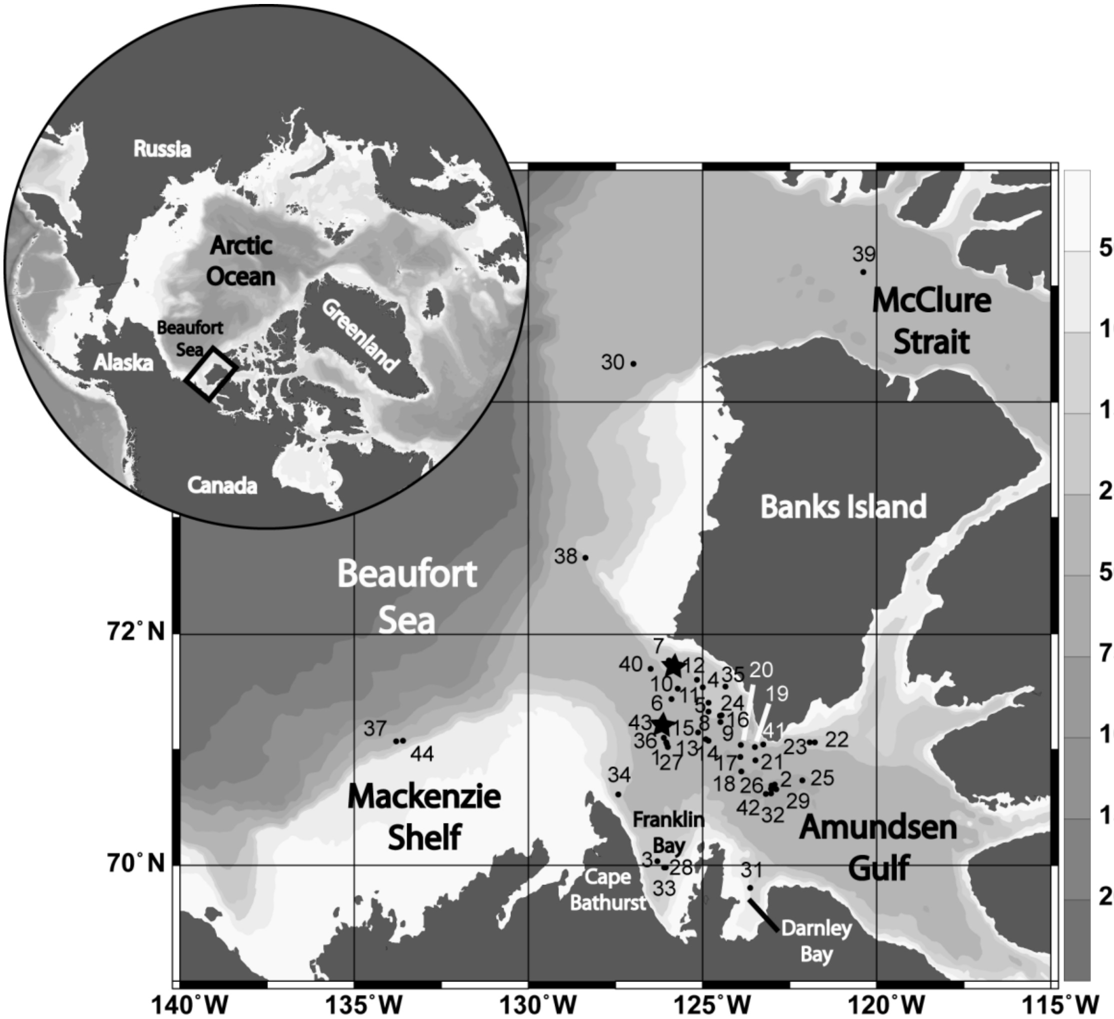


Figure 4.1. Bathymetry of the southeastern Beaufort Sea with the location of zooplankton sampling stations. Stations are numbered in chronological order of sampling. The stars indicate the location of the mooring stations CA-08 (to the south) and CA-16 (to the north).

4.4.2 Sampling

Zooplankton sampling was conducted from the research icebreaker CCGS *Amundsen* between 24 October 2007 and 30 July 2008 at 44 stations in the southeastern Beaufort Sea (Figure 4.1). The majority of stations (35) were located in western Amundsen Gulf, and the remaining sites were sampled along the northwest coast of Banks Island, the Mackenzie Shelf, Darnley Bay and Franklin Bay.

A SBE911 plus® CTD and a Seapoint® fluorometer attached to the rosette sampler provided profiles of salinity, temperature and *in situ* fluorescence. The chlorophyll *a* (chl *a*) concentrations determined for water samples taken at discrete depths were used to calibrate the *in situ* fluorescence signal. Weekly ice coverage of Amundsen Gulf for 2007-2008 was extracted from the Canadian Ice Service archives using the IceGraph Version 1.03 application (http://ice-glaces.ec.gc.ca/IceGraph103/page1.jsf).

Depth-stratified samples for the assessment of zooplankton biomass and respiration were obtained by deploying a 0.50-m^2 square aperture Hydrobios® multinet sampler carrying nine nets of 200 µm mesh size each fitted with a 2-L rigid codend with filtration apertures located at the top of the cylinder. The sampler was hauled vertically at 0.5 $m\ s^{-1}$ from 10 m above the sea floor to the surface. Three 20-m depth strata were sampled from 10 m above the bottom upward and three from 60 m to the surface. The remaining interval from 70 m above the bottom to 60 m below the surface was divided in three equal sampling strata, the thickness of which depended on station depth. For example, the nine depth strata sampled in succession from 10 m above bottom to the surface at a 430 m deep station were: 420-400, 400-380, 380-360, 360-260, 260-160, 160-60, 60-40, 40-20, 20-0 m.

Upon retrieval, macrozooplankton (e.g. large amphipods, euphausiids, medusae and fish larvae) were removed from the samples, as they are not sampled quantitatively by the Hydrobios. The samples were subdivided in quarters using a Motoda splitting box in a cold room (0°C). Two quarters from each codend were allocated to respiration and biomass measurements respectively. The remaining half was preserved in a borax-buffered seawater solution of 4% formaldehyde for later taxonomic analysis. The subsample was diluted in filtered seawater at 0°C and kept at 0°C until the measurement of respiration based on enzymatic assay.

To calibrate the enzymatic assays, additional live zooplankton was collected for the direct measurements of respiration using a polarographic electrode at 17 stations in the Amundsen Gulf from late February to late July 2008. A 1-m^2 square aperture vertical sampler with a 200-µm mesh net and a 2-L rigid codend was towed vertically from 10 m above the bottom to the surface at 0.5 m s^{-1}. The sampler was lowered codend-first to avoid filtering on the way down. Upon recovery, the content of the codend was diluted in filtered seawater and cnidarians were removed to reduce zooplankton mortality. The sample was kept at 0°C until respiration was measured both by the polarographic electrode method and the ETS assay (see below).

4.4.3 Respiration

The enzymatic activity of the Electron-Transfer-System (ETS), an index of respiration, was determined using the ETS assay method developed by Båmstedt (2000). For each assay, live zooplankton samples from the nine depth layers were fractionated into 200-1000 and >1000 µm size classes, and then homogenized directly with an INT (*p*-iodonitrotetrazolium violet) reagent following precisely the protocol of Båmstedt (2000). The homogenates were incubated for one hour at 40°C after which the reaction was stopped with a quench solution (50% formaldehyde and 50% phosphoric acid). A blank of INT reagent without biological material received the same treatment. After adding 1 mL of chloroform/methanol (2:1 by volume), the sample was mixed before centrifugation at 3000 rpm for four minutes. The lower phase was completed to 3 mL with methanol before a second centrifugation. The reaction colour was measured at 475 nm against the blank. Standards for the transformation of measured ETS activity into respiration (µg O_2 h^{-1}) were prepared according to Båmstedt (2000) for each batch of reagents used over the quasi-annual duration of the study.

The relatively quick and easy ETS assay enabled us to estimate relative respiration on board for the 362 samples making up the 41 vertical profiles. To validate the ETS measures and transform enzymatic activity into actual respiration, live zooplankton was incubated for the direct measure of respiration using a polarographic electrode. At 17 stations from late February to late July, a fraction of the live sample was poured into a funnel equipped with a 1000 µm sieve and a gate valve. The volume of water above the sieve was maintained constant and at maximum level by adding filtered seawater at 0°C. The large size class was retained in this volume of water in the top part of the device while the small size class was slowly evacuated through the sieve with the filtered seawater, recovered delicately in a container and stored at 0°C prior to incubation. Each of the two size fractions was gently split into three equal triplicates and, after verifying visually that the animals were in good condition, each triplicate was introduced into a separate glass bottle (473 mL capacity) that was then filled to the brim with filtered seawater at 0°C and capped. Simultaneously, control bottles without zooplankton were prepared in triplicates. The triplicates for the two size classes and the control were incubated for 24-48 hours in the dark at 0°C. Dissolved oxygen concentration in the control bottles was measured with a polarographic electrode before and after incubation to verify for possible changes. At the end of the experiment, the difference in oxygen concentration between animal-free control bottles and incubation bottles was assumed to be the zooplankton respiration, divided by the duration of the incubation to obtain the hourly (ml O_2 h^{-1}) or daily (ml O_2 d^{-1}) oxygen consumption R_O. To avoid a potential effect of oxygen depletion on respiration, only the triplicate batches where average saturation exceeded 70% at the end of the incubation were retained. At the end of the incubation, ETS activity was determined in each triplicate, following the assay described above. The equation of the regression of R_O on ETS for the 200-1000 µm and >1000 µm mesozooplankton fractions was used to convert ETS profiles into daily oxygen consumption profiles.

Daily oxygen consumption R_O (ml O_2 d^{-1}) was converted to daily respiratory carbon loss R_C (mg C d^{-1}) using:

$$R_C = R_O \text{ x } RQ \text{ x } 12/22.4, \qquad (1)$$

where RQ (respiratory quotient) is the molar ratio of carbon produced to oxygen consumed, 12 is the molecular weight of carbon and 22.4 is the molar volume of carbon dioxide at standard temperature and pressure (Ikeda et al. 2000). Assuming a metabolism primarily based on proteins, a RQ of 0.97 (Gnaiger 1983) was used at all times for the small fraction and during the season of high pelagic primary production for the large fraction. A RQ of 0.75 was applied to the large zooplankton during the overwintering period when metabolism is fuelled predominantly by lipid reserves (Ingvarsdóttir et al. 1999).

4.4.4 Biomass and taxonomy

At sea, the aliquot for total zooplankton biomass was size fractionated on a 1000-µm sieve and rinsed thoroughly with filtered seawater. The 200-1000 and >1000 µm size classes were placed on Nitex screens and carefully blotted with absorbing material before freezing at -20°C. On land, the samples were transferred to pre-weighed plastic cups and oven-dried at 60°C for 48 h prior to dry weight measurement on a high precision (± 1 µg) microbalance. For a given station, the weighted mean depth of the zooplankton biomass was calculated as $\Sigma(w_i d_i z_i)/\Sigma(d_i z_i)$, where w_i is the dry weight of zooplankton within depth interval *i*, d_i is the thickness of depth interval *i*, and z_i is the midpoint depth of the interval.

In the laboratory, the formalin-preserved subsamples for taxonomy were size fractionated on a 1000-µm sieve and re-suspended in distilled water. Known aliquots were taken from the small and large fractions using a Henson-Stempel pipette and a Motoda splitting box, respectively, to obtain approximately 300 animals that were counted, measured and identified to species or to the lowest taxonomic resolution attainable. Carbon content for each species was estimated using published length-mass relationships for arctic zooplankton following Hopcroft et al. (2005), Mumm (1991), and Forest et al. (Forest et al. 2011a). Zooplankton community structure and the vertical distribution and population dynamics of key species are the focus of Chapter 2. Only the general taxonomy and biomass of the two size fractions of zooplankton are presented here.

4.5. Results

4.5.1 Sea ice, temperature and chlorophyll

Sea-ice extent in SE Beaufort Sea in September 2007 was the lowest on record since 1979, and the study area was essentially ice-free at the end of summer. Starting in early November, young and new ice formed rapidly, filling most of the eastern Amundsen Gulf. Consolidation into >80% first-year ice was completed by December (Figure 4.2a). The ice cover remained dynamic throughout winter and ice concentration seldom reached 100% while substantial amounts (up to 28%) of new ice formed in winter flaw leads. Sea ice started to break-up in early May, about one month earlier than average (Barber et al. 2010), followed by a decline in ice cover extent from 90% in early May to less than 5% in early July (Figure 4.2a).

The three water masses typical of the highly stratified Beaufort Sea were detected in the temperature profiles of all stations along the track of the ship except the shallowest (Figure 4.2b). Atmospheric forcing strongly influenced the Polar-Mixed Layer (PML) that extended from the surface to ~50 m depth. At the onset of ice formation in October, surface temperature was close to freezing point and remained so until ice break-up in May. Then the PML warmed rapidly to reach temperatures above 8^{o}C in the 0-20 m layer in July. The steep Pacific Halocline (PH) extended from the PML to about 200 m with an inverse temperature gradient from -1.6 to 0^{o}C at 200 m. The warmer Atlantic Waters with temperatures > 0^{o}C extended from 200 m to the bottom.

In late October, the depth of the chlorophyll maximum (Z_{CM}) was located around 25 m, with concentrations up to 1 µg chl *a* L^{-1} (Figure 4.2c). As the ice cover formed in November, fluorescence declined below the detection limits of the probe before increasing again in late April when concentrations above 0.1 µg chl a L^{-1} were measured in the top meters of the water column,

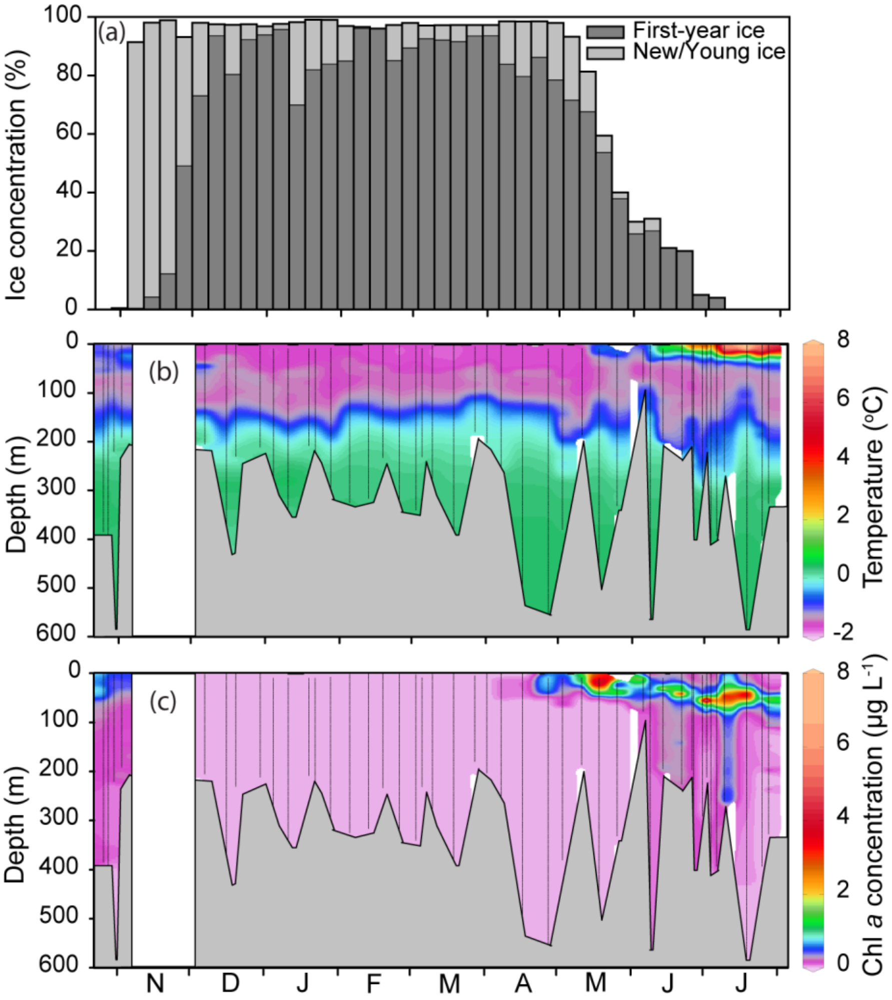


Figure 4.2. Time series of ice concentration in Amundsen Gulf (a) and corresponding time-depth sections of temperature (b) and chl a concentration (c) along the track of the ship from October 2007 to August 2008.

Tableau 4.1. Abundance and biomass of the main zooplankton taxa integrated over the water column and averaged over the period October 2007 to July 2008 in Amundsen Gulf. Means and standard deviations are given.

	Abundance (number m^{-2})	Biomass (g C m^{-2})
200-1000 µm fraction		
Calanus glacialis (CI-CIII)	7 676 ± 6338	0.280 ± 0.214
Metridia longa (CI-CIV)	11 160 ± 8445	0.174 ± 0.148
Pseudocalanus spp. (CI-CV)	10 772 ± 6974	0.025 ± 0.015
Oithona similis (CIV-F)	35 314 ± 18904	0.022 ± 0.012
Triconia borealis (CV-F)	18 772 ± 11394	0.022 ± 0.014
Microcalanus spp. (CIII-F)	9 451 ± 4429	0.012 ± 0.006
Others*	9 013 ± 5384	0.044 ± 0.054
Total	102 158 ± 45705	0.579 ± 0.340
>1000 µm fraction		
Calanus hyperboreus (CIII-F)	1 564 ± 869	2.104 ± 1.231
Calanus glacialis (CIV-F)	4 898 ± 3100	0.785 ± 0.500
Metridia longa (CV-F)	5 033 ± 4623	0.531 ± 0.491
Carnivores***	1 164 ± 1058	0.537 ± 0.551
Mesopelagic and deep copepods**	593 ± 526	0.071 ± 0.068
Others****	641 ± 725	0.084 ± 0.092
Total	13 893 ± 8167	4.112 ± 2.171

* Others (small fraction) include primarily *Oncaea* sp., Bivalves, *Limacina helicina*, *Clione limacina*, *Scolecithricella minor* by decreasing order of abundance;

** Mesopelagic and deep copepods include primarily *Aetideopsis rostrata*, *Gaetanus tenuispinus*, *Gaidius* spp. by decreasing order of abundance;

*** Carnivores include primarily *Paraeuchaeta glacialis*, *Eukronhia hamata*, *Dimophyes arctica*, *Parasagitta elegans*, *Aglantha digitale* by decreasing order of abundance;

**** Others (large fraction) include primarily *Boroecia maxima, Limacina helicina* by decreasing order of abundance.

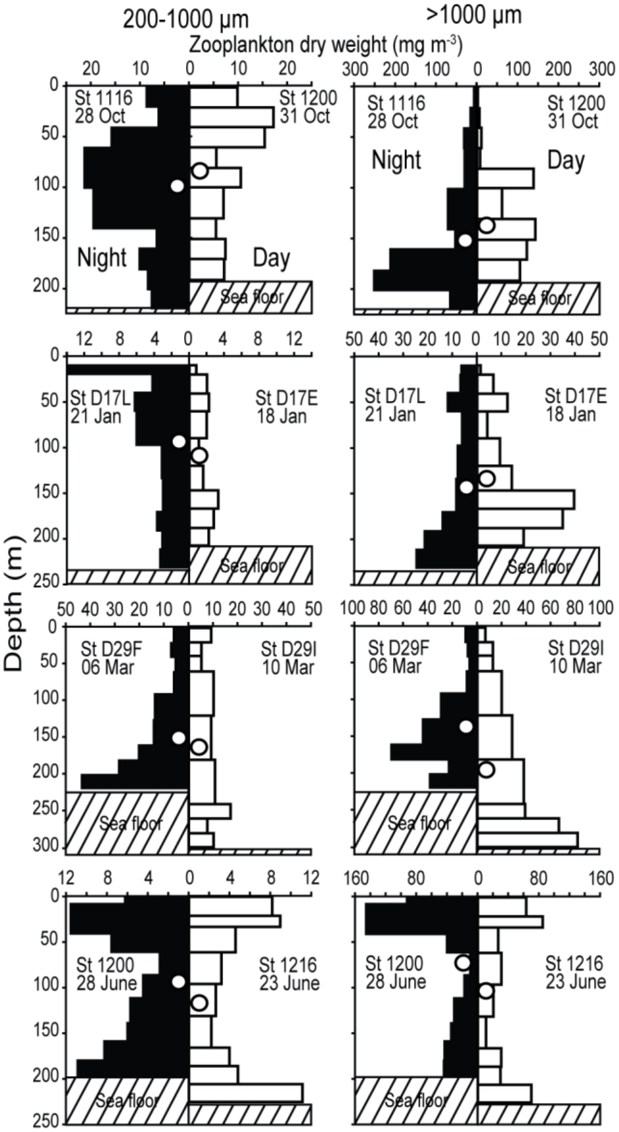


Figure 4.3. Nighttime (closed histograms) and daytime (open histograms) vertical distribution of zooplankton biomass for the 200-1000 µm (left panels) and >1000 µm (right panels) fractions at selected stations in Amundsen Gulf. Open circles correspond to the weighted mean depth of the biomass distribution.

presumably coinciding with the sloughing off of ice algae as ice melt started. Microalgal biomass increased in May (9.8 µg chl *a* L^{-1} peak at a Z_{CM} of 15 m) as the ice cover rapidly receded. After this first bloom, fluorescence values decreased to <1 µg chl *a* L^{-1} for most of June then bounced back in July, forming a subsurface chl *a* maximum (SCM) at about 55 m depth (Figure 4.2c).

4.5.2 Zooplankton composition, biomass, and diel vertical migration

The composition of the mesozooplankton was typical of Arctic waters with a strong dominance of copepods (Table 4.1). On average over the year, the small fraction (200-1000 µm) was 7.4 times more numerous than the large fraction (>1000 µm), but its biomass was 7.1 times less. *Calanus glacialis* copepodites CIII and young *Metridia longa* (CI-CIV) represented 48 and 30% respectively of the biomass in the small fraction. *Calanus hyperboreus* was the main contributor (51%) to biomass in the large fraction, followed by *C. glacialis* (19%) and *Metridia longa* (13%).

The comparison of day and night profiles of biomass in different seasons failed to show any extensive diel vertical migration by either the small or the large fraction of zooplankton (Figure 4.3). In all seasons, the biomass of the small fraction was distributed relatively uniformly over the water column and the position of the weighted mean depth changed little between day and night. The biomass of the large zooplankton fraction was concentrated at depth in all seasons except summer (June) and vertical distribution changed little between day and night. The small differences in weighted mean depth between daytime and nighttime profiles reflected differences in station depth rather than any diel migration (Figure 4.3).

4.5.3 ETS activity and respiration

R_o, the respiration measured directly by the polarographic electrode method was linearly correlated to ETS, the enzymatic activity of the Electron-Transfer-System (Figure 4.4). The slope of the regression did not differ significantly between the two size classes ($t = 0.44$, $P = 0.666$). However, the intercept was significantly higher ($t = -2.27$, $P = 0.031$) in the small fraction than in the large (Figure 4.4). Phytoplankton, in particular chain-forming diatoms, was retained on the 200-µm sieve, but not on the 1000-µm sieve. As well, the ratio R/ETS was weakly correlated to chl a concentration in the 0-60 m depth strata for the 200-1000 µm zooplankton fraction ($r^2 = 0.32$, $n = 14$, $P = 0.036$), but not for the >1000 µm fraction. Hence, the higher intercept of the regression of R_o on ETS in the small fraction likely reflected a slight overestimation of R_o due to phytoplankton respiration during incubation in the dark. Given the difference in intercept, the data for the two fractions were not pooled and ETS was transformed into respiration using the separate regression for each fraction.

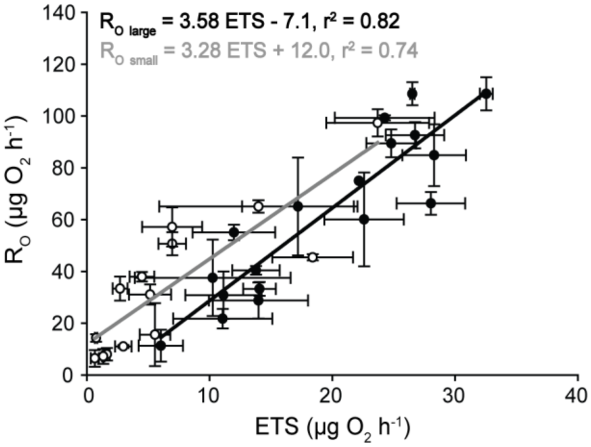


Figure 4.4. Regression of respiration (R_o, measured by polarographic electrode) on Electron-Transfer-System activity (ETS) for the 200-1000 µm (open symbols) and >1000 µm fraction (closed symbols) of zooplankton. Each data point is the average of triplicates with horizontal and vertical range bars corresponding to one standard deviation for the two variables respectively.

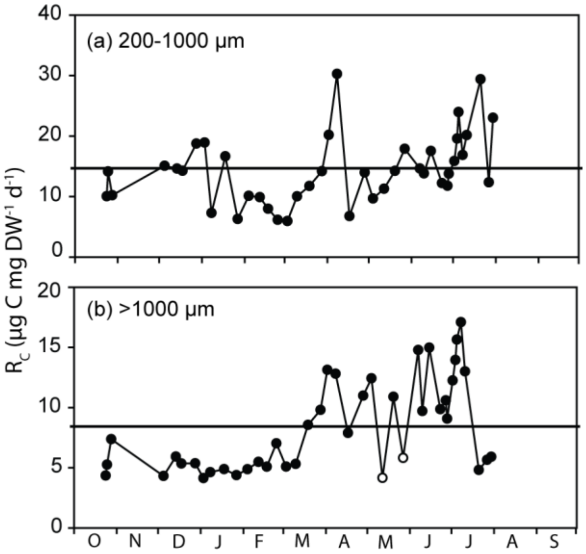


Figure 4.5. Time series of daily specific respiratory carbon loss for the small (a) and large (b) fractions of zooplankton collected in the southeastern Beaufort Sea from October 2007 to July 2008. Horizontal lines correspond to the mean over the 10-month time series. The open symbols in (b) indicate values at stations outside the Amundsen Gulf.

4.5.4 Seasonal variability in specific respiration

On average over the quasi-annual cycle, the production of respiratory carbon per unit biomass was higher in the small zooplankton fraction (14.4 ± 5.7 µg C mg DW^{-1} d^{-1}) than in the large fraction (8.4 ± 4 µg C mg DW^{-1} d^{-1}) (Figure 4.5). Specific respiratory carbon loss was variable in small zooplankton with values generally below the mean from January to May, except for a peak in early April (Figure 4.5a). The seasonal pattern was clearer in large zooplankton, with specific carbon production remaining low from October to mid-March (5.2 ± 0.9 µg C mg DW^{-1} d^{-1}), and then nearly doubling from mid-March to mid-July (11.3 ± 3.2 µg C mg DW^{-1} d^{-1}), before reverting in late July to low values comparable to the fall-winter rates (Figure 4.5b).

4.5.5 Spatio-temporal distribution of zooplankton biomass and community respiration

As expected, zooplankton community respiration (R_c, as C loss) was strongly related to biomass (B) for the small fraction ($\ln R_c = -2.388 + 0.563 \ln B$, n = 317, $r^2 = 0.671$, $P < 0.0001$) and the large fraction ($\ln R_c = -4.370 + 0.909 \ln B$, n = 328, $r^2 = 0.728$, $P < 0.0001$). Spatially, the depth-integrated community respiration of the small fraction varied little across the study area (Figure 4.6a). Variations were weakly but significantly correlated to depth ($r^2 = 0.16$, $P = 0.0097$). The much higher community respiration of the large fraction was also correlated to depth ($r^2 = 0.27$, $P = 0.0006$) and reached maximum values in the deep central channel of Amundsen Gulf (Figure 4.6b).

Temporally, the depth-integrated community respiration R_c was minimum from December to mid-January for the two size fractions of zooplankton (Figure 4.7). In the small fraction, R_c increased rapidly from late January to March and then declined progressively until the end of summer (Figure 4.7a). High values occurred in October. In the large fraction, depth-integrated community respiration increased irregularly from late January to July (Figure 4.7b). Relatively high values were also recorded in October.

Temporally and vertically, the distribution of community respiration was closely related to the distribution of biomass (Figures 4.8 and 4.9). From December to March, the small biomass of the small zooplankton fraction (200-1000 µm) tended to increase and was distributed relatively uniformly over depth (Figure 4.8a). As a result, respiration increased uniformly in the water column over the winter months (Figure 4.8b). From mid-April to early November, the small zooplankton fraction invaded the 0-50 m surface layer (Figure 4.8a), and community respiration for this size class took place primarily near the surface (Figure 4.8b).

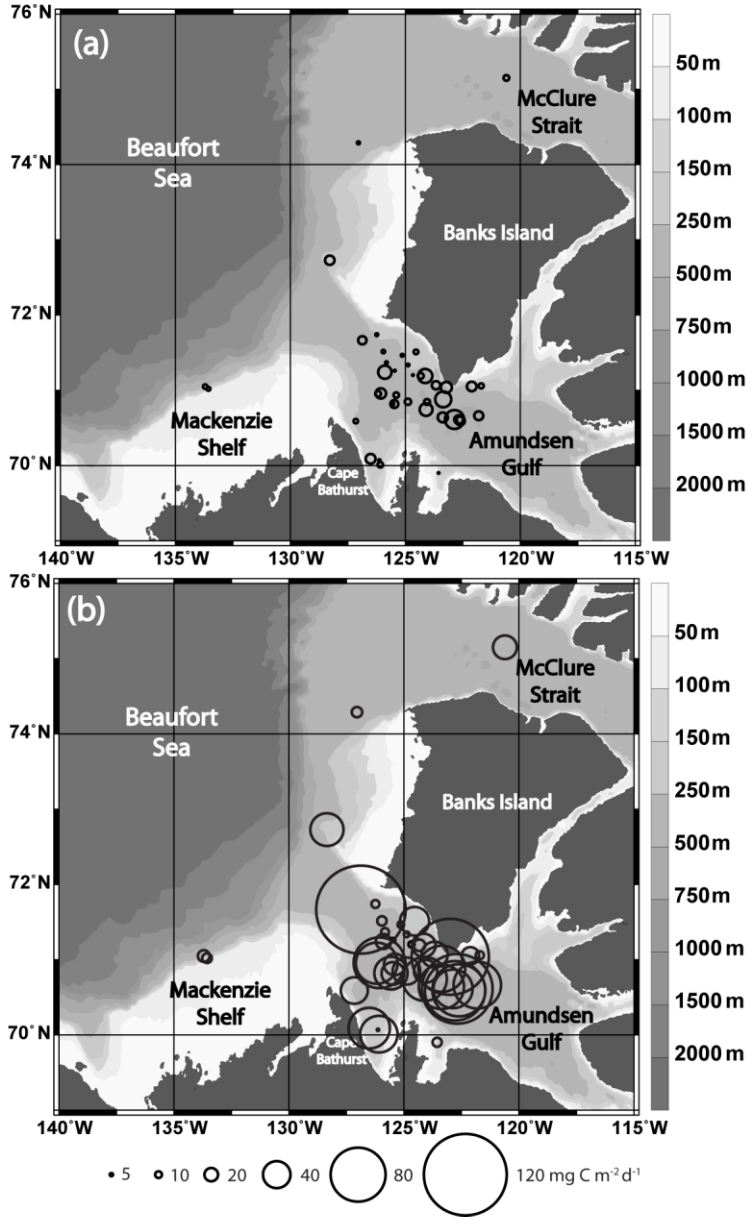


Figure 4.6. Spatial distribution of the vertically-integrated community respiration (R_c, as respiratory carbon loss) for the 200-1000 µm (a) and the >1000 µm zooplankton fractions in the southeastern Beaufort Sea from 24 October 2007 to 30 July 2008.

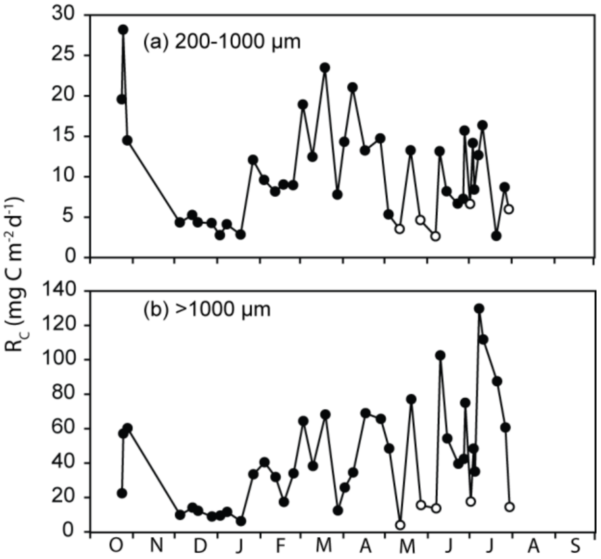


Figure 4.7. Time series of depth-integrated daily respiratory carbon loss (R_c) for the small (a) and large (b) fractions of zooplankton collected in the southeastern Beaufort Sea from October 2007 to July 2008. The open symbols indicate stations outside the Amundsen Gulf.

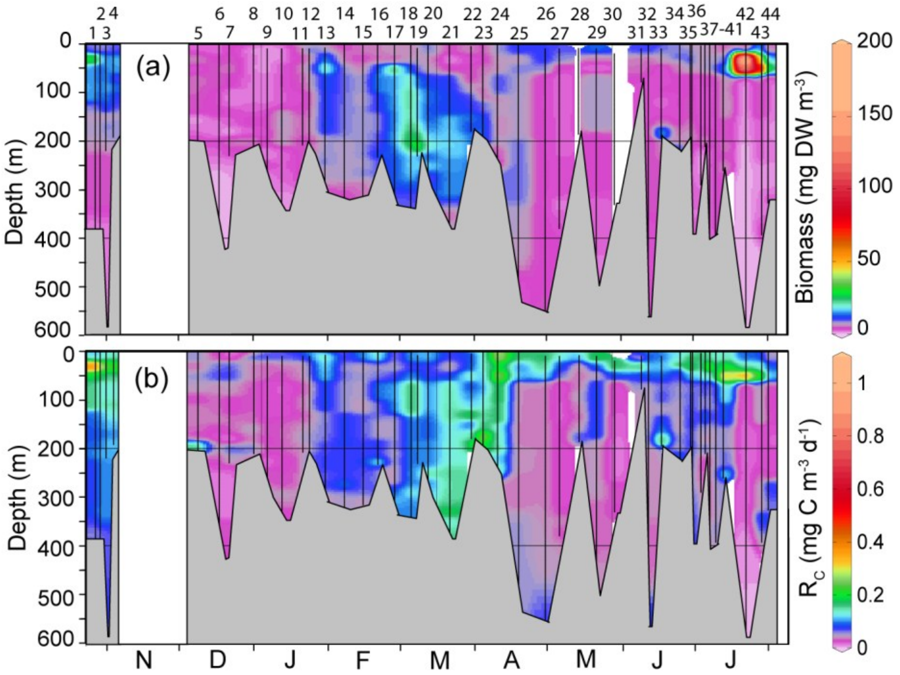


Figure 4.8. Time-depth section of biomass (a) and community respiration as carbon loss (b) for the 200-1000 µm zooplankton size fraction in the southeastern Beaufort Sea from October 2007 to July 2008. Vertical lines correspond to the date of biomass and respiration profiles. White surfaces indicate missing data. Numbers on top refer to stations in Figure 4.1.

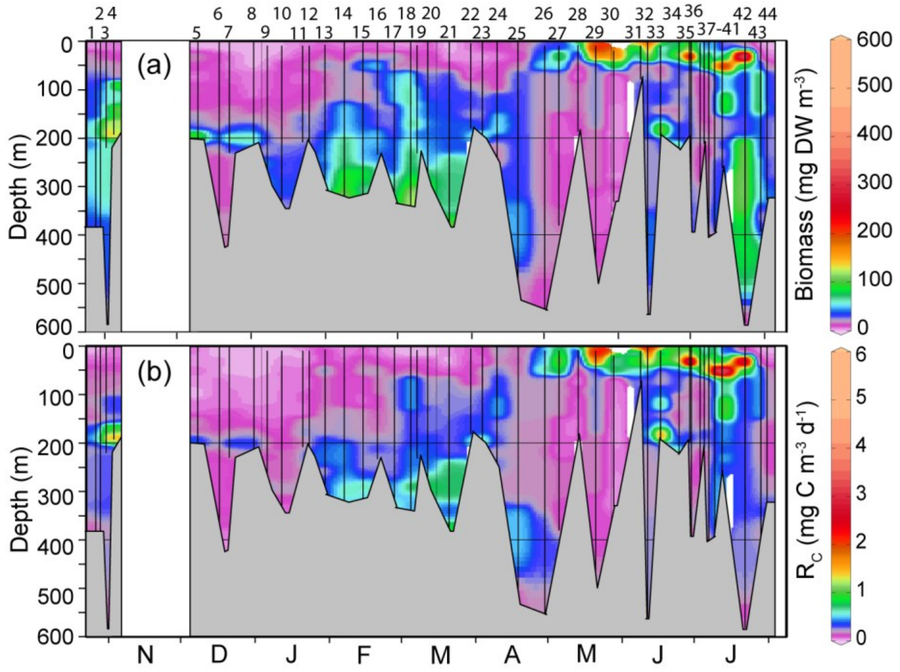


Figure 4.9. Time-depth section of biomass (a) and community respiration as carbon loss (b) for the >1000 µm zooplankton size fraction in the southeastern Beaufort Sea from October 2007 to July 2008. Vertical lines correspond to the date of biomass and respiration profiles. White surfaces indicate missing data. Numbers on top refer to stations in Figure 4.1.

Large zooplankton were concentrated in the deep basins of Amundsen Gulf from December to late April, then congregated in the surface layer (0-50 m) from early May to early July, and started their downward migration in July (Figure 4.9a). By October, the large zooplankton fraction was again concentrated at depth. The time-depth distribution of community respiration R_c followed essentially the same seasonal pattern as biomass (Figure 4.9b).

4.6. Discussion

4.6.1 Zooplankton community respiration in polar seas

Measures of zooplankton community respiration are few for the Arctic Ocean. Welch et al. (1997) used large respiration chambers to incubate non-fractionated live zooplankton assemblages >202 µm in repeated experiments over an annual cycle in shallow Resolute Passage (Canadian Arctic Archipelago). Specific respiratory carbon loss varied from 5.5 to 23.4 µg C mg DW^{-1} d^{-1} over the year, a range commensurate with that reported here for the 200-1000 µm (5.9-30.3 µg C mg DW^{-1} d^{-1}) and >1000 µm (4.1-17.1 µg C mg DW^{-1} d^{-1}) zooplankton fractions in Amundsen Gulf. Our estimates of specific respiration also fall within the range 4-80 µg C mg DW^{-1} d^{-1} measured by Alcaraz et al. (2010) for the whole zooplankton assemblage collected along a transect from Fram Strait to Svalbard in July 2007. In the Southern Ocean, mesozooplankton size fractions of 200-500, 500-1000 and >1000 µm off the Antarctic Peninsula respired at average rates of 12.6 ± 6.0, 26.2 ± 20.1 and 24.3 ± 15.5 µg C mg DW^{-1} d^{-1} respectively in December (southern hemisphere summer) (Hernández-León et al. 1999). These values compare well with rates of 18.1 ± 5.7 and 12.7 ± 2.8 µg C mg DW^{-1} d^{-1} for the 200-1000 and >1000 µm zooplankton fractions respectively when averaged over the corresponding summer period in the Amundsen Gulf. Based on the tight regression between ETS activity and direct respiration measurements, and the good agreement between our estimates of specific respiration and those reported for other polar seas, we conclude that our respiration estimates based on this new ETS enzymatic approach are reliable. As expected, biomass was a good predictor of zooplankton community respiration. Hence, the respiration-biomass linear relationships presented here represent a potentially useful tool to estimate zooplankton respiration from dry weight.

4.6.2 Zooplankton control of pelagic primary production

In the Beaufort Sea, relatively large diatoms dominate both the ice algal production in spring and the spring-summer phytoplankton bloom (Forest et al. 2008; Riedel et al. 2008). To quantify the impact of zooplankton grazing on primary production, we first translated respiration (R) into a rough estimate of ingestion (I), assuming an assimilation and a gross growth efficiency of 70% and

30% respectively: I = 100R/(70-30) = 2.5R (Ikeda et Motoda 1978). Estimated ingestion confirms that the large calanoid herbivores making up the bulk of the >1000 µm fraction were responsible for most (89%) of total zooplankton ingestion in the top 100 m in spring and summer. Large calanoid herbivores ascended from their deep overwintering habitat in late April, a month ahead of the ice break-up (defined as 50% ice cover) in late May. In the interval between the vernal recolonization of the surface layer and the ice break-up that triggered the phytoplankton bloom, the mesozooplankton presumably fuel carbon demand from several sources including the low concentration of ice algae sloughed from the melting sea ice, a precocious under-ice phytoplankton production (Forest et al. 2011b), and microzooplankton (Seuthe et al. 2007).

Based on nutrient drawdown from February to July 2008, Forest et al. (2011b) estimated gross primary production (GPP) at 40-65 g C m^{-2} in the euphotic layer of areas deeper than 250 m in the Amundsen Gulf. Assuming 24-h grazing in the 0-100 m layer of the same sector, zooplankton consumption between May and July accounted on average for 11.3 ± 4.0 g C m^{-2} or 17-28% of GPP. This estimate of the fraction of GPP intercepted by zooplankton in the euphotic zone of Amundsen Gulf in spring-summer overlaps the 22-44% derived from faecal pellet carbon flux in northern Barents Sea (Wexels Riser et al. 2008). By comparison, in Baffin Bay, copepods and appendicularians grazed an estimated 52% of GPP between April and July 1998 in the surface layer of the highly productive eastern North Water (Tremblay et al. 2006), while the *Calanus* complex (*C. hyperboreus, C. glacialis,* and *C. finmarchicus*) intercepted between 13 and 93% of primary production during the phytoplankton bloom from May to early June in Disko Bay (Madsen et al. 2001).

By contrast to the spring-summer period, algal cells <5 µm typically dominate the subsurface chlorophyll maximum in the southeastern Beaufort Sea in late fall (Brugel et al. 2009; Tremblay et al. 2009; Martin et al. 2010). In October 2007, picophytoplankton <5 µm made up 75% of the microalgal assemblage (M. Ardyna, unpublished data, 2011). A dominance of small phytoplankton cells favours grazing by microzooplankton and small mesozooplankton to the detriment of large calanoid herbivores that specialize on large cells (Brugel et al. 2009; Tremblay et al. 2009; Martin et al. 2010). Based on respiration, the 200-1000 µm zooplankton fraction was responsible for 64% of the POC grazed by the overall mesozooplankton in the surface 100 m in the fall. Primary production was not measured in the fall of 2007, but (Brugel et al. 2009) provide an estimate of 20-40 mg C m^{-2} d^{-1} for late October-early November 2003 in Amundsen Gulf. Assuming a similar primary production in the two years, a daily GPP of 20-40 mg C m^{-2} d^{-1} would have satisfied the carbon demand of the 200-1000 µm zooplankton fraction (20.2 ± 5.2 mg C m^{-2} d^{-1}, or 51-101% of daily GPP) in 2007, but could not sustain the metabolic carbon demand (105 ± 51 mg C m^{-2} d^{-1}) of the abundant assemblage of large calanoid copepods that had already left the surface layer and migrated to depth. Small pellets largely dominate the vertical faecal POC flux in fall and early winter in the Beaufort Sea (Forest et al. 2007; Forest et al. 2008), an observation that confirms that small mesozooplankton are the main grazers of phytoplankton biomass during this period.

Total mesozooplankton ingestion (200-1000 + >1000 µm fractions) integrated over the entire water column amounted to 23.5 ± 7.5 g C m^{-2} or 36-59% of the estimated 40-65 g C m^{-2} GPP integrated over spring-summer. For comparison, total ingestion by microzooplankton (5-200 µm) over the same period was estimated at 15.6 g C m^{-2} or approximately 30% of GPP by Forest et al. (2011b). Therefore, based on respiration, we conclude that the large (>1000 µm) *Calanus* herbivores and *Metridia longa* active in the surface layer in spring and summer are the major consumers of primary production over the annual cycle of the pelagic food web of Amundsen Gulf, as reported for other arctic regions (Rysgaard et al. 1999; Tremblay et al. 2006). In the fall, the 200-1000 µm mesozooplankton fraction, made up at 42% of juvenile CIII of *C. glacialis*, was primarily responsible for the grazing of the weak primary production in the surface layer.

4.6.3 Active carbon export by *Calanus*

Not all respiration at depth by zooplankton actually contributes to the active transport of carbon from the surface layer to depth. For instance, respiration at depth by non-migrant omnivores feeding on sinking particles or by non-migrant carnivores does not accelerate the export to depth of the POC produced in the surface layer. In offshore arctic seas, large ontogenetic migrants such as late copepodite stages and adult *Calanus* that build up large lipid reserves are presumably responsible for most of the active export of carbon to depth (Hirche 1997; Auel et al. 2003). Hence, the combined respiration at depth of *C. hyperboreus* and *C. glacialis* >1000 µm is likely a conservative estimate of active carbon transport. Given the tight correlation between respiration and biomass for the >1000 µm fraction, respiration by *Calanus* below 100 m can be calculated by pro-rating overall zooplankton respiration by the biomass of *Calanus*. This approach first assumes that *Calanus* do not feed at depth in winter. Stable isotope analyses and grazing experiments have confirmed the true herbivorous nature of *C. hyperboreus* (Campbell et al. 2009; Forest et al. 2011a), and winter feeding at depth is unlikely for this species. *C. glacialis* sometimes preys on heterotrophs (e.g. Campbell et al. 2009), but the low specific respiration rate of large zooplankton at depth from October to mid-March supports the notion that basal metabolism and egg maturation in winter were fuelled essentially by endogenous reserves. Pro-rating respiration by biomass also assumes that specific respiration rates of *Calanus* are similar to those of other large zooplankton. From February to early April 2004, the specific respiration of *C. hyperboreus* and *C. glacialis* under the landfast ice of Franklin Bay was 4.1 ± 0.04 and 6.2 ± 0.9 µg C mg DW^{-1} d^{-1}, respectively (G. Darnis, unpublished results based on the separate incubation of the two species, 2004). These values are close to the mean specific respiration rate of the large size class in early winter 2007-2008 (5.2 ± 0.9 µg C mg DW^{-1} d^{-1}), which supports our assumption that the two *Calanus* species respire at rates similar to those of other large zooplankton in winter.

Based on the above, mean active vertical carbon transport by *Calanu*s was estimated at 3.1 ± 2.1 and 2.5 ± 1.7 g C m^{-2} below 100 m and 200 m respectively for the period 24 October-17 April in regions of Amundsen Gulf deeper than 250 m. Active transport of carbon beyond 100 m represented approximately 85% of the POC passive flux at 100 m recorded from 24 October to 28 July at Station CA-08 (M. Sampei, unpublished data, 2010) and 132% of the passive flux for the same period at Station CA-16 (Sampei et al. 2012). Our estimate of active transport of carbon beyond 100 m by *Calanus* is close to the lower limit of the range of annual gravitational POC fluxes (3.3-6.0 g C m^{-2} yr^{-1}) at Station CA-08 for 2004, 2005 and 2006 (Forest et al. 2010). No POC flux was recorded at 200 m in 2007-2008. However, our estimate of active carbon transport beyond this depth falls in the range of annual gravitational POC fluxes recorded at 200 m in the deepest region of Amundsen Gulf (1.9-3.8 g C m^{-2} yr^{-1}) and at Station CA-08 (1.3-2.3 g C m^{-2} yr^{-1}) for 2004, 2005 and 2006 (Lalande et al. 2009b). Overall, the active downward transport of carbon linked to the seasonal migration of *Calanus* species in Amundsen Gulf was of the same magnitude as the annual passive POC flux, which stresses the importance of the seasonal migration of arctic zooplankton in the downward transport of organic carbon.

4.7. Conclusion

Longhurst and Williams (1992) calculated that, at the scale of the North Atlantic, the active transport of carbon by the ontogenetic migration of *C. finmarchicus* was only 0.1% of the gravitational flux at 200 m, and concluded that this transport could therefore be neglected in carbon budgets. At odds with their results for the North Atlantic, our analysis of the time-depth distribution of size-fractionated mesozooplankton respiration over an annual cycle in Amundsen Gulf confirms the importance of the seasonal ontogenetic migrations of *Calanus* in actively transporting organic carbon from the surface layer to depth in Arctic seas (Hirche 1997; Auel et al. 2003). Conservatively, active carbon transport by the seasonal migration of zooplankton was of the same magnitude as the gravitational flux of POC. Therefore it should be included in future synthesis of carbon fluxes in the Arctic Ocean. The divergence between the conclusions of Longhurst and

Williams (1992) and ours certainly stems in part from (1) the large gravitational fluxes prevailing in the Atlantic Ocean (10-58 g C m^{-2} yr^{-1} at 150 m) (Morales 1999) relative to the Arctic Ocean (1.6-5.9 g C m^{-2} yr^{-1} at 200 m) (Lalande et al. 2009b), and (2) the large body size and lipid reserves of *C. hyperboreus* and *C. glacialis* compared to *C. finmarchicus* (e.g. Scott et al. 2000). We suspect however that the difference in the importance of the respiratory carbon fluxes generated by the *Calanus* complex in the two regions is ultimately linked to the different light regimes prevailing at high and temperate latitudes. By feeding near the surface at night and descending at depth in daytime, the zooplankton of temperate and tropical oceans actively export some carbon at depth on a daily basis (Longhurst et Williams 1992). In Arctic seas, the diel cycle of night and day does not occur outside brief periods around the equinoxes. It is replaced by the annual cycle of polar night and midnight sun, which is responsible for the extreme seasonality of arctic primary production. Obviously, seasonal ontogenetic migrations and the remarkable capacity of arctic zooplankton (in particular *Calanus hyperboreus*) to delay the remineralisation of organic matter by storing it into large lipid reserves are adaptations forced by the pulsed nature of arctic microalgal production (e.g. Falk-Petersen et al. 1990). The observed strong downward flux of carbon is a by-product of the combination of widespread annual migrations and exceptionally large lipid reserves in arctic zooplankton. We conclude that the importance of the active transport of carbon by zooplankton relative to the gravitational flux reported here for the Amundsen Gulf is ultimately rooted in the annual photoperiod (as opposed to diel) prevailing in the Arctic.

5. Chapitre 5 – Conclusion générale

L'échantillonnage stratifié du mésozooplancton, en mer de Beaufort pendant l'Année Polaire Internationale 2007-2008, m'a donné une opportunité sans précédent de définir l'implication de la respiration et de la migration de taxons dominants de l'assemblage zooplanctonique dans le fonctionnement de la pompe biologique d'un écosystème océanique arctique. À ma connaissance, la seule autre étude couvrant à la fois des cycles quasi-annuels de biomasse et de respiration zooplanctonique arctique est celle de Welch et al. (1997) menée au centre de l'archipel arctique canadien. Seulement, l'absence de résolution verticale de la distribution de la biomasse et de la respiration empêche l'usage de ces données pour quantifier l'exportation de carbone généré par les déplacements du zooplancton. Également sans stratification verticale, les quelques rares autres mesures de respiration du zooplancton arctique ne représentent en outre que des instantanés de quelques semaines dans l'année, quand le retrait estival de la glace facilite l'accès à ces sites (Hirche 1987; Ikeda et Skjoldal 1989; Takahashi et al. 2002a; Auel et al. 2003; Alcaraz et al. 2010). Pour la même raison, notre connaissance sur la distribution verticale du zooplancton est majoritairement circonscrite à la saison de couverture minimale de glace de mer.

Les campagnes d'échantillonnage russes et américaines menées à partir de stations de glace dérivantes dans les bassins arctiques pendant les années 1950-70 (Johnson 1963; Dawson 1978; Vinogradov 1997), ou à leur périphérie en 1997-98 avec le projet SHEBA (Ashjian et al. 2003), ont fourni l'essentiel de l'information disponible sur les fluctuations saisonnières de la distribution verticale du zooplancton. Ces études pionnières se sont cantonnées à la simple description des patrons de migration verticale d'espèces jugées importantes. Mon étude constitue une contribution significative à notre compréhension des mécanismes qui régulent la distribution verticale du zooplancton dans les milieux océaniques arctiques. Elle identifie l'utilisation possible de gradients de température de l'eau ainsi que des stratégies d'alimentation distinctes expliquant la répartition des copépodes dominants dans les eaux stratifiées de la mer de Beaufort. Cette thèse met également en exergue le rôle déterminant de la migration du copépode *Calanus hyperboreus* dans le flux de carbone vers les profondeurs océaniques de l'Arctique et détaille son cycle de reproduction et de développement lors d'une année de faible couverture de glace.

5.1. Répartition verticale des copépodes dominants dans le golfe d'Amundsen

5.1.1 Migrations interzonales des *Calanus* arctiques

Le premier volet de la thèse (chapitre 2) avait pour objectif d'examiner les variations saisonnières de la distribution verticale de sept copépodes qui dominent le zooplancton arctique et d'en étudier les facteurs déterminants, dans notre cas la température et la nourriture. Les résultats de notre étude démontrent en premier lieu que la translocation saisonnière de la biomasse totale du mésozooplancton observée dans le golfe d'Amundsen est principalement due à la migration de *Calanus hyperboreus* (Figures 2.3a et 2.4b). Dans la partie centrale profonde du golfe, nous pouvons estimer l'amplitude du mouvement saisonnier de cette population à environ 200 m. Ceci en fait la migration interzonale la plus extensive des sept taxons sous étude (Figure 5.1). Le fait que la majorité de la population hivernante de *C. hyperboreus* se tienne dans la couche Atlantique est notable pour la durée de séquestration du carbone qui a été exporté de la zone euphotique par la migration et relâché dans la couche la plus profonde lors de la respiration. L'autre grand herbivore du système, *Calanus glacialis*, effectue également une migration saisonnière classique. Toutefois, nos résultats indiquent que la profondeur d'hivernage de cette espèce, reconnue comme néritique comparativement à l'océanique *C. hyperboreus*, dépasse rarement la base de l'Halocline Pacifique.

Les résultats du chapitre 2 montrent d'autre part que la descente saisonnière des deux *Calanus* arctiques vers les couches profondes légèrement plus chaudes que la surface n'est pas liée à une quête de refuge thermique froid où le métabolisme de base, et donc la perte d'énergie, seraient réduits. L'hypothèse de l'avantage métabolique, proposée pour expliquer la migration saisonnière de leur congénère boréal *Calanus finmarchicus* en Atlantique nord (Ingvarsdóttir et al. 1999), n'est donc pas transposable aux *Calanus* endémiques des systèmes arctiques où les gradients de température sont bien plus faibles et en partie inversés en hiver. Passant allègrement des températures positives (jusqu'à +0,3°C) de leur habitat profond d'hivernage à des températures proches du point de congélation (-1,7°C) de la surface, lors de leur ascension printanière, nous concluons que c'est la haute saisonnalité de la production de cellules microalgales à la base de leur alimentation, plus que le gradient de température ambiante, qui dicte la migration saisonnière de ces grands herbivores. En outre, l'évitement de la prédation est un des aspects à prendre en compte pour expliquer leur retrait en profondeur quand la production primaire décline. Une explication supplémentaire, proposée pour le cas de *C. hyperboreus* dont la reproduction hivernale se déroule en profondeur, est que les femelles recherchent ces températures un peu plus élevées afin de stimuler la maturation gonadique.

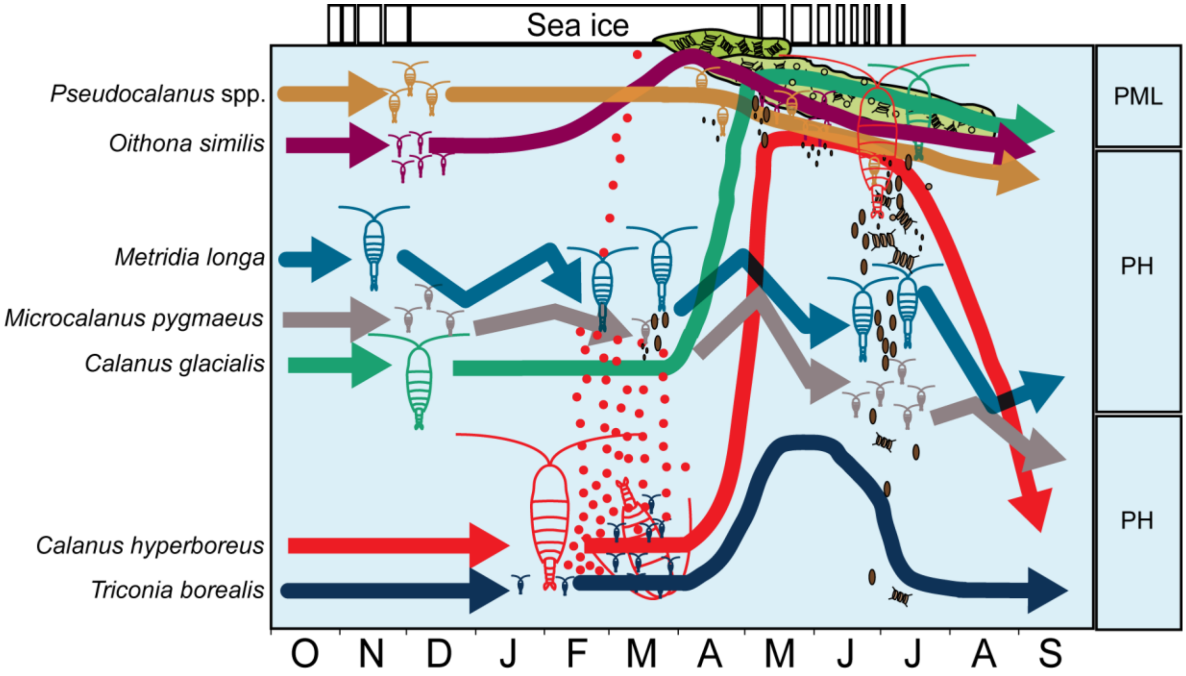


Figure 5.1. Schématisation de la variation saisonnière de la distribution verticale et des interactions trophiques des sept copépodes dominant l'assemblage du zooplancton arctique du Golfe d'Amundsen.

5.1.2 Les déplacements saisonniers de faible amplitude des petits copépodes

D'après nos résultats, les cinq autres copépodes considérés emploient des stratégies de migration caractérisées par des déplacements verticaux de faible ampleur, ce qui souligne leur importance moindre dans le transport actif de carbone (Figure 5.1).

L'ascension saisonnière progressive qui a amené le petit copépode omnivore *Oithona similis* proche de la surface, au moment du pic de biomasse d'algue de glace, s'est produite sur une courte distance de part et d'autre de la bordure supérieure froide (-1,6°C) de l'Halocline Pacifique. Une association a pu aussi être faite entre la position de cette isotherme froide et la distribution des copépodes *Pseudocalanus* spp. pendant la saison englacée. Ces espèces cryophiles, distribuées à l'année longue dans la zone épipélagique froide, dépendent certainement de la production primaire de la zone euphotique. Cependant leur alimentation hivernale dans cette zone alors appauvrie en carbone organique particulaire demeure un mystère. Persister en surface à ces basses températures peut être vu comme une stratégie visant à réduire le métabolisme de base pendant une longue période de disette.

Cette étude a aussi mis en lumière une possible association entre le petit copépode détritivore mésopélagique *Triconia Borealis* et *Calanus hyperboreus*, les seuls copépodes du lot à fréquenter assidument la couche Atlantique en hiver (Figure 5.1). Une brève incursion de *T. borealis*, jusqu'à des profondeurs intermédiaires situées dans l'Halocline Pacifique, a coïncidé avec l'ascension saisonnière du grand herbivore à la fin avril. Nous proposons qu'en hiver ce petit détritivore couvre une partie de sa demande en carbone en s'alimentant sur des carcasses de femelles de *Calanus hyperboreus* mortes de sénescence après leur ultime saison de production (Sampei et al. 2012).

5.1.3 Migrations ontogénétiques et stratégies d'embuscade des copépodes mésopélagiques

L'examen de la distribution verticale des omnivores *Metridia longa* et *Microcalanus pygmaeus*, entre l'Halocline Pacifique et la couche Atlantique, démontrent leur appartenance au domaine mésopélagique sur l'ensemble du cycle annuel (Figure 5.1). Cependant, pour chacune des deux espèces, une répartition verticale selon les stades de développement a été indicatrice d'une migration ontogénétique dans cet intervalle intermédiaire de la colonne d'eau. *M. longa* est un opportuniste qui se nourrit d'une grande variété de proies. D'après nos observations et celles rapportées antérieurement (Conover et Huntley 1991), ce copépode intercepte une partie des œufs de *Calanus hyperboreus* qui flottent vers la surface pendant la saison de reproduction (janvier-début avril; chapitre 3) de cette espèce, et passe à un régime plus herbivore au déclenchement de la production primaire (Forest et al. 2011a). Le régime alimentaire du plus petit *Microcalanus pygmaeus* n'est, à proprement parler, pas connu. Cependant des similarités entre la forme des mandibules des deux espèces laissent supposer qu'elles partagent les mêmes stratégies d'alimentation. Nous proposons donc une stratégie d'embuscade permettant à ces deux copépodes d'exploiter à la fois les particules flottant vers la surface, tels que les œufs riches en lipides de *C. hyperboreus*, et les amas de microalgues et de détritus provenant des couches superficielles de l'océan. Quant au phénomène de migration ontogénétique, nous offrons de l'expliquer à l'aide de la théorie de la stratégie optimale de recherche de la nourriture (MacArthur et Pianka 1966). Ainsi, le recours aux mêmes sources limitées de nourriture, et/ou les risques de compétition pour ces ressources et de cannibalisme, amènent les animaux à s'éparpiller en proportion de la disponibilité de nourriture dans le but de réduire la pression de compétition et d'optimiser les gains énergétiques individuels (Fortier et Harris 1989).

5.1.4 Effet de la température sur la distribution des copépodes

S'appuyant sur 181 estimations de taux de croissance de différentes espèces de copépodes vivant à des températures variant entre -1,7^{o}C et 30^{o}C, Huntley et Lopez (1992) démontrent que la température ambiante explique à elle seule plus de 90% de la variance du taux de croissance de ces organismes. Une prédiction logique découlant de cette forte relation est qu'à la saison libre de glace, les copépodes arctiques recherchent les températures relativement plus élevées des eaux de surface, réchauffées par les radiations solaires estivales, afin d'augmenter leur activité métabolique. Toutefois, nos observations sur la distribution de tous les taxons sous étude vont à l'encontre de cette prédiction alors que l'historique des températures vécues par tous ces copépodes était variable. Qui plus est, la lentille de surface, avec des températures comprises entre 0 et 8^{o}C, était plutôt moins fréquentée que des couches sous-jacentes plus froides. La pente de la relation croissance-température étant faible dans la fourchette de températures inférieure à 10^{o}C, nous concluons que ces espèces arctiques gagnent peu à se distribuer dans la zone éclairée et plus chaude en surface. Il n'en demeure pas moins que la croissance et le développement des copépodes sont étroitement dépendants de la température (Huntley et Lopez 1992). Cependant, la distribution verticale des sept copépodes dominant le zooplancton de la mer de Beaufort devrait découler de la mise en œuvre de compromis visant à optimiser l'ensemble des paramètres responsables de leur valeur adaptative (fitness) sur la totalité du cycle vital, et non seulement l'activité métabolique et la production biologique immédiate en lien avec la température ambiante (Varpe 2012). L'information détaillée que la présente étude amène à propos des différents stades de développement sera sans nul doute utile pour modéliser l'impact des changements de température attendus sur la croissance, le développement et la survie de ces espèces arctiques importantes.

5.1.5 Cycle vital et reproduction de Calanus hyperboreus dans le golfe d'Amundsen

Ma thèse fournit des informations précieuses sur la dynamique annuelle de la population et la reproduction du grand copépode *Calanus hyperboreus*, l'espèce clé des réseaux trophiques des régions océaniques (>200 m de profondeur) de l'Océan Arctique. À l'aide d'un modèle individu-centré, Ji et al. (2012) suggèrent que, malgré son adaptation à la grande variabilité de la production primaire arctique, cette espèce peine à garder des populations viables dans les bassins centraux englacés quasi en permanence. Certaines années, une saison de croissance trop courte pour permettre le développement au premier stade capable d'hiverner (CIII) aboutirait à l'échec du recrutement de ce copépode. Ces auteurs proposent que les stocks de *C. hyperboreus* de l'Arctique central sont maintenus grâce à l'advection d'individus produits dans certaines zones des mers marginales. En dépit de son statut panarctique, des aspects importants de l'écologie de *C. hyperboreus* n'avaient jusqu'à présent été examinés que dans quelques-unes de ces zones périphériques de l'Arctique (détroit de Fram, baies de Disko et de Resolute), et de façon partielle. Le chapitre 3 ajoute le sud-est de la mer de Beaufort à cette base de connaissances et constitue la première étude à décrire une saison complète de reproduction hivernale chez cette espèce.

L'observation de la population hivernante, dominée par les stades CIV et plus âgés, suggère que les conditions de croissance pendant la saison de production biologique de 2007 ont été favorables aux jeunes stades de l'année. Une longue saison de croissance due au record de minimum de glace de 2007 aura permis à une majorité de ceux-ci d'atteindre le stade CIV en l'espace d'une année. Nous pouvons ainsi estimer à deux ou trois ans la durée du cycle annuel de la population de *Calanus hyperboreus* dans la région d'étude, soit un temps de génération comparable à ce qui est proposé pour des régions connaissant normalement des conditions de glace moins sévères (Polynie des Eaux du Nord et baie de Disko).

Nos mesures de taux de production d'œufs démontrent également que *C. hyperboreus* a connu une reproduction vigoureuse, de janvier à début avril 2008, si on la compare à l'hiver 2004 dans la proche baie de Franklin, ou encore à des mesures effectuées dans le détroit de Fram. Cette reproduction dans la couche Atlantique profonde, en avance du lancement de la saison de production primaire, a donc été alimentée par d'importantes réserves lipidiques emmagasinées lors de la précédente saison 2007. La disparition hâtive de la glace au printemps, un mois plus tôt que la normale, et la forte production primaire subséquente (Forest et al. 2011b) ont permis aux femelles adultes en 2008 de refaire leurs réserves lipidiques en l'espace de deux mois. Elles ont pu ainsi entamer la descente à leur profondeur d'hivernage au milieu de l'été, bien avant la fin de la saison de production primaire.

Paradoxalement, nos résultats révèlent que, en dépit de la forte production d'œufs et des conditions d'alimentation apparemment favorables du début de la saison, le recrutement des jeunes stades CI a été particulièrement faible dans le golfe d'Amundsen en cette année de faible concentration de glace. Étant donnée la brièveté du délai entre la fin de la reproduction et l'efflorescence phytoplanctonique, nous ne privilégions pas ici l'hypothèse du risque d'un décalage entre l'arrivée des premiers stades capables de s'alimenter et la disponibilité de nourriture pour expliquer ce recrutement médiocre. La conséquence de ce dernier a été une stagnation de l'abondance et la biomasse de la population de *Calanus hyperboreus* dans le golfe pendant l'été. En revanche, le copépode mésopélagique omnivore *Metridia longa* a été particulièrement abondant dans le golfe en 2007 et 2008, sans doute en réponse à la relaxation du régime de glace jusqu'à tard en automne 2007. Les Metridinidés étant des prédateurs voraces des œufs de copépodes, nous suggérons que *M. longa* a pu limiter la croissance de la population de *C. hyperboreus* dans le golfe d'Amundsen en s'attaquant aux œufs et nauplii de cet herbivore lors de leur ascension vers la surface. Eu égard à cette proposition, la conclusion du chapitre 3 est que l'allongement de la saison libre de glace, attendu avec le réchauffement rapide de l'Arctique, peut amener le risque de l'intensification du contrôle descendant, exercé par des omnivores mésopélagiques plus abondants, sur les populations de *C. hyperboreus*. Un tel débalancement des interactions trophiques au sein de la communauté zooplanctonique pourrait contrecarrer les bénéfices potentiels pour l'espèce clé *C. hyperboreus* d'une augmentation de la production primaire à la marge des plateaux continentaux arctiques, avec des conséquences prévisibles pour les flux gravitationnels (pelotes fécales) et actifs de carbone dans ces systèmes.

5.2. La respiration du zooplancton et la pompe biologique

5.1.1 Transport actif de carbone par la migration saisonnière des *Calanus* arctiques

Un des points saillants de cette thèse est sans conteste l'établissement de l'importance considérable du processus de transport de carbone par la migration saisonnière du zooplancton pour le fonctionnement de la pompe biologique d'un écosystème oligotrophe arctique. Les résultats du chapitre 4 indiquent que la respiration du carbone préalablement fixé en surface et transporté en dessous de 100 et 200 m dans les réserves lipidiques des *Calanus* arctiques est du même ordre de grandeur que les flux gravitationnels annuels de carbone organique particulaire atteignant ces profondeurs. Cette contribution majeure de grands migrateurs saisonniers du genre *Calanus* à l'exportation de carbone en profondeur se compare bien à celle d'autres Calanidés, cette fois-ci du genre *Neocalanus*, dominant la biomasse zooplanctonique dans les systèmes également oligotrophes nord-Pacifique et austral (Tableau 1.1). Au même titre que pour ces régions, nous concluons qu'il est important d'ajouter ce transport actif par la migration des *Calanus* aux futures synthèses des flux de carbone de l'Océan Arctique.

À l'échelle de l'Atlantique nord, Longhurst et Williams (1992) ont toutefois calculé un flux actif de carbone, du à la migration saisonnière du copépode *Calanus finmarchicus*, ne formant que 0,1% du flux gravitationnel, et ont déclaré qu'il pouvait donc être négligé dans les bilans de carbone. Encore selon ces chercheurs, les migrateurs verticaux nycthéméraux seraient les principaux médiateurs du transport de carbone dans cette région considérée comme eutrophe. Nous expliquons cette contradiction entre leur conclusion et ce qui est observé dans les systèmes oligotrophes arctique, nord-Pacifique et austral par un flux gravitationnel plus important dans l'Atlantique nord, ainsi que par les réserves lipidiques plus imposantes des *Calanus* arctiques et *Neocalanus* pacifiques par rapport au plus petit *C. finmarchicus* nord-atlantique.

Les patrons saisonniers de migration verticale présentés au chapitre 2 révèlent que le flux actif dans la couche Atlantique (sous 200 m) est essentiellement du à la perte de carbone par la respiration des représentants de *Calanus hyperboreus* lors de leurs 7-9 mois d'hivernage. La respiration de *Calanus glacialis* contribue principalement au flux actif dans la couche de 100 à 200 m comprenant une partie de l'Halocline Pacifique. Le temps de résidence de l'eau Pacifique (~ 50-200 m) étant de 11 ans (Yamamoto-Kawai et al. 2008), et celui des couches Atlantique et profondes (>250 m) de 30 à 300 ans (Gregor et al. 1998) en mer de Beaufort, Nous pouvons conclure que *C. hyperboreus* a un rôle autrement plus décisif que son congénère dans la séquestration à moyen et long terme du carbone. Ainsi, une distribution hivernale de cette espèce au delà de 1000 m de profondeur, telle qu'observée dans le détroit de Fram, conduirait à un stockage de carbone hors de l'atmosphère pour quelques centaines d'années. Afin d'évaluer l'ampleur de ce processus à l'échelle de l'Océan Arctique, il convient de mieux définir la distribution profonde hivernale de *C. hyperboreus* sur une grande partie de son aire de distribution géographique.

5.1.2 Régulation de l'exportation du carbone

Dans la présente étude, nous avons calculé à partir des données de respiration que l'ensemble du zooplancton a ingéré 36-59% de la production primaire brute réalisée pendant la période printemps-été de forte productivité biologique. Ce résultat confirme le rang du zooplancton comme premier consommateur de la production primaire pélagique des écosystèmes océaniques arctiques. Sans surprise, c'est la grande fraction de taille (>1 mm), largement dominée par les herbivores *Calanus hyperboreus*, *C. glacialis* et dans une moindre mesure l'omnivore *Metridia longa*, qui assure l'essentiel (89%) de l'interception de carbone biogène pendant la période de mai à juillet. En revanche, nos résultats démontrent aussi que le petit zooplancton prend le relais de la consommation et du recyclage du carbone en surface en automne après que les grands copépodes *Calanus* aient complété leur migration saisonnière vers les profondeurs et soient entrés en phase de repos métabolique (diapause).

5.3. Perspectives de recherche

Cette thèse met en lumière le rôle important des déplacements du zooplancton en temps que moteur de la pompe biologique de CO_2 au sein d'un écosystème pélagique arctique oligotrophe, et produit de l'information précieuse sur les patrons de migration verticale et la biologie de composantes clés de la communauté zooplanctonique. Dans le même temps, certaines interprétations de ces résultats auraient certainement nécessité d'être plus fermement étayées par des connaissances de base actuellement manquantes, notamment sur le régime alimentaire de la plupart des espèces. Donc, sans surprise, nos travaux ouvrent de nouvelles perspectives de recherche:

1) Dans cette thèse, grand cas est fait du rôle crucial du grand herbivore *Calanus hyperboreus*, aussi bien dans le flux respiratoire de carbone, que dans l'apport hivernal de matière organique sous forme de carcasses et d'œufs, aux mésopélagiques *Metridia longa*, *Microcalanus pygmaeus* et *Triconia borealis*. Cependant, en l'absence de données qualitatives et quantitatives sur l'alimentation de ces omnivores/détritivores opportunistes, l'interaction prédateur-proie proposée ici avec l'herbivore demeure spéculative. Il est donc impératif de concevoir des expériences visant à étudier la trophodynamique de ces espèces. Par exemple, il faudrait reproduire avec *M. longa* et des œufs de *C. hyperboreus* l'expérience d'alimentation de Sell et al. (2001) qui a révélé le fort taux d'ingestion appliqué par *Metridia lucens* sur les œufs de *Calanus finmarchicus* dans l'Atlantique nord. Avec de telles données, le contrôle descendant d'une espèce arctique sur l'autre pourrait être vérifié.

2) Une autre approche pour étudier les interactions entre *Calanus hyperboreus* et *Metridia longa* est d'exploiter des séries temporelles multiannuelles sur le zooplancton qui commencent à s'étoffer dans l'Arctique canadien grâce aux efforts d'échantillonnage réalisés au sein du réseau de centres d'excellence ArcticNet. Dans l'observatoire à long terme établi en mer de

Beaufort, ce sont déjà 10 ans qui ont été couverts, en comptant l'échantillonnage réalisé pendant le projet CASES de 2002 à 2004. Il serait intéressant de suivre les démographies respectives des deux espèces. Par l'emploi de cette méthode, Plourde et al. (2003) fait le lien entre le décuplement de l'abondance de *M. longa* et la diminution de moitié du stock de *C. hyperboreus* entre 1979-1980 et 1994-1998 dans l'estuaire de St Laurent.

3) En regard de sa contribution significative à l'abondance et à la biomasse des communautés zooplanctoniques, et de son impact potentiel sur une autre espèce clé arctique, le cycle biologique de *Metridia longa* devrait être mieux documenté qu'il ne l'est présentement. Cela est d'autant plus nécessaire que cette espèce opportuniste pourrait répondre rapidement à la relaxation des conditions environnementales dans les mers englacées, comme cela semble avoir été le cas en 2007-2008 dans le golfe d'Amundsen. Les riches banques de données des projets CASES (2003-2004) et CFL (2007-2008), agrémentées de mesures de production d'œufs non encore publiées, offrent une opportunité exceptionnelle d'étudier cette espèce dans le sud-est de la mer de Beaufort sur un cycle annuel.

4) Cette étude révèle la contribution élevée des migrateurs saisonniers *Calanus* (particulièrement *C. hyperboreus*) au flux de carbone dans le golfe d'Amundsen, une région profonde du plateau continental, et il serait salutaire de chercher à vérifier si tel est le cas dans d'autres régions océaniques arctiques. Avec suffisamment de points répartis correctement à travers la méditerranée arctique, il serait alors possible de tenter un bilan panarctique de ce processus de transport actif de carbone, comme cela a été fait sur une vaste zone ($55{,}6\ 10^{6}\ \mathrm{km}^{2}$) de l'Océan austral où $0{,}17\ \mathrm{Gt\ C\ an}^{-1}$ est amené en profondeur par le copépode *Neocalanus tonsus* (Bradford-Grieve et al. 2001). Bradford-Grieve et al. (2001) ont révélé que ce grand copépode, lors de sa migration saisonnière, transportait en dessous de 300 m de profondeur une quantité de carbone de 14% supérieure à celle interceptée par des pièges à particules placés à cette profondeur. En Arctique, une telle entreprise nécessiterait un effort d'échantillonnage colossal afin de collecter les informations sur la biomasse des migrateurs herbivores dans leur habitat profond d'hivernage et sur la durée de cette période. Mais une fois ces profils de biomasse obtenus, il serait relativement facile de déterminer le flux respiratoire de carbone en appliquant la relation respiration-biomasse du grand zooplancton établie dans notre étude (Chapitre 4).

5) Dans cette thèse, le rôle des migrations verticales nycthémérales n'a pas été considéré, argüant du fait que ces déplacements de la part du mésozooplancton ne se réalisent que sur de courtes

distances (Figure 4.3; Runge et Ingram 1991; Tourangeau et Runge 1991; Fortier et al. 2001; Blachowiak-Samolyk et al. 2006). Toutefois, des études menées au nord de la mer de Barents, et basées sur des données acoustiques, démontrent des mouvements journaliers de zooplancton pouvant transporter du carbone sous la zone euphotique de cette région influencée par l'Atlantique (Cottier et al. 2006; Berge et al. 2009; Wallace et al. 2010). Bien que ces déplacements n'alimentent pas un flux respiratoire très profond, le transport actif puis l'émission de carbone sous forme de pelotes fécales en dehors de la zone de rétention maximale contribuent à renforcer le flux gravitationnel de carbone organique particulaire (Hernández-León et al. 2001). Les animaux impliqués dans ces migrations nycthémérales ne sont pas formellement identifiés mais les euphausidés et amphipodes composant le macrozooplancton sont les candidats privilégiés (Berge et al. 2009), soit une fraction de taille non prise en compte par notre échantillonneur multiséquentiel. Il serait donc intéressant, d'une part, de vérifier l'existence de telles migrations dans notre partie de l'Arctique à partir du même type de données acoustiques, et d'autre part, de qualifier les migrants du macrozooplancton à l'aide de filets adaptés, le cas échéant.

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