Table des matières

Résumé iii

Liste des tableaux vi

Liste des figures vii

Remerciements ix

Avant-propos x

1. Introduction générale 1
  1.1. Le contexte Arctique 1
  1.2. Écosystèmes marins arctiques 2
  1.3. Le phytoplancton arctique 4
  1.4. Le zooplancton arctique 5
  1.5. Le métabolisme des lipides 6
  1.6. Problématique et objectifs de recherche 8

2. Diapause as functional trait of a biogeochemical model of an Arctic pelagic ecosystem. 10
  2.1. Résumé 10
  2.2. Abstract 11
  2.3. Introduction 12
  2.4. Model description 15
    2.4.1. Diapause implementation 15
    2.4.2. Respiration and excretion 16
    2.4.3. Ontogenic vertical migration 17
    2.4.4. Model modification 18
    2.4.5. Model configuration 24
    2.4.6. Calibration 26
    2.4.7. Validation 27
    2.4.8. Sensitivity analysis 27
  2.5. Results 27
    2.5.1. Environmental dynamic 27
    2.5.2. Parametrization of respiration and nitrogen excretion 28
    2.5.3. Diapause dynamics 28
    2.5.4. Trophic relationships 33
    2.5.5. Implications for planktonic production 34
    2.5.6. Sensitivity analysis 35
  2.6. Discussion 37
    2.6.1. Realistic allometric relationships 37
    2.6.2. Realistic diapause phenology 38
  2.7. Conclusion 42

3. Conclusion générale 43
  3.1. Changement de phénologie 44

3.2. Impact sur la biomasse totale planctonique 45
3.3. Futures implications 47
4. Bibliographie 50

Liste des tableaux

Table 1 : List of the functional metazoan parameters 23
Table 2 : Sensitivity of the timing of entry and exit of diapause for the numerical mesozooplankton species (#48). 36

Liste des figures

Figure 1 : Différente phénologies phytoplanctoniques le long d'un gradient latitudinal en Arctique..........3
Figure 2 : Schéma du réseau trophique retrouvé en Arctique 4
Figure 3 : Trophic network of our configuration of the model...........20
Figure 4 : Study location within the Arctic...........22
Figure 5 : Post spin-up annual cycle of the model...........25
Figure 6 : Migration pattern of the copepod-like numerical species of 1635 µm of diameter that exhibits a recurring realistic diapause pattern...........29
Figure 7 : Comparison of the numerical metazoans metabolisms with the literature data.. 30
Figure 8 : Migration pattern and C:N dynamic (orange line) over one year for the copepod-like #48 (a) biomass dynamic over the thermocline in summer and early fall (b).. 30
Figure 9 : Trophic network of our configuration of the model...........32
F**igure 10** : Impact of the diapause trait on the phenology..........34
Figure 11 : Impact of the diapause on the biomasses 35
Figure 12 : Sensitivity analysis on the metazoan compartment...........36
Figure 13 : Distribution mondiale et biomasse d'espèces fonctionnelles d'une configuration de DARWIN sans le trait fonctionnel de la diapause. 46
Figure 14 : Proportion de différents stades ontogéniques de Calanus hyperboreus présent dans des pièges à sédiments au large de la mer de Beaufort.. 48
Figure 15 : Pompe à lipide et « court-circuit lipidique » (lipid shunt)..........49

"However, I continue to try and I continue, indefatigably, to reach out. There's no way I can single-handedly save the world or, perhaps, even make a perceptible difference - but how ashamed I would be to let a day pass without making one more effort."

~ Isaac Asimov

Remerciements

Je tiens à remercier mon superviseur Frédéric Maps qui m’a conseillé et aiguillé tout au long du processus de recherche scientifique. Je tiens à remercier tous les membres de NÉOLab pour leurs conseils et leur soutien lors du déroulement de mes recherches. Je remercie aussi le Professeur Stephanie Dutkiewicz pour ses conseils, ses encouragements ainsi que pour m’avoir invité à présenter mes recherches dans le cadre prestigieux de son laboratoire au MIT à Boston.

Je remercie aussi tous les étudiants du bureau 4085 pour les discussions enrichissantes qui m’ont ouvert à d’autres perspectives et points de vue de ma recherche. Je remercie tout particulièrement Kevin Ma pour son soutien, ses réflexions et ses conseils sur la rigueur de la démarche scientifique.

Je remercie le pôle océanographique Québec-Océan et le réseau de centres d’excellence du Canada ArcticNet pour leurs soutiens financiers ainsi que tous les employé(e)s et étudiant(e)s faisant partie de ces organismes avec qui j’ai pu échanger.

Cette deuxième maîtrise m’a permis de parfaire mes connaissances en Océanographie des milieux extrêmes et d'approfondir encore plus mes capacités de compréhension et d’analyse de données environnementales et écologiques. Je remercie toutes les personnes de mon entourage qui m’ont soutenues psychologiquement pendant cette aventure polaire numérique : Ma mère, qui a toujours cru en moi; mon père qui m’a toujours soutenu, quelles que soit les circonstances; ma grande sœur et ma petite sœur qui toutes deux ont toujours été là pour me remonter le moral; mon chat Bragi. Finalement, je tiens à remercier ma conjointe Joeva, qui a été mon roc et qui m’a poussée à ne pas lâcher durant ces deux dernières années.

Avant-propos

Ce mémoire de maîtrise comporte une introduction générale ainsi qu'une conclusion en français. Le corps du mémoire a été rédigé en anglais sous la forme d'un article scientifique au vu d'une publication future.

Les résultats issus de ce projet de recherche ont fait l'objet de communications scientifiques durant des congrès nationaux et internationaux :

Pourchez A., Maps F. (2017). Impact of the diapause trait on the dynamics of plankton communities in a numerical pelagic Arctic ecosystem. Présentation orale donnée lors de la conference internationale ArcticChange2017 ayant eu lieu à Québec, Canada.

Pourchez A., Dufresne C., Maps F. (2017). Impact of the implementation of the diapause trait on the dynamics of plankton communities in a numerical pelagic Arctic ecosystem. Présentation invitée devant l'équipe DARWIN au MIT à Boston, USA.

Pourchez A., Dufresne C., Maps F. (2017). Impact of the implementation of the diapause trait on the dynamics of plankton communities and the carbon cycle in a numerical pelagic Arctic ecosystem. Présentation orale donnée lors de la conférence internationale Advances in Marine Ecosystem Modelling Research ayant eu lieu à Plymouth, Angleterre.

Pourchez A., Maps F. (2017). Impact de l'ajout du trait de diapause sur le cycle du carbone et la phénologie dans un écosystème numérique pélagique arctique. Présentation orale présentée lors du colloque de biologie du Département de Biologie de l'Université Laval à Québec, Canada.

Pourchez A., Dufresne C., Maps F. (2016). Impact de l'implémentation de la diapause sur la dynamique des assemblages de populations numériques de planctons arctiques. Poster présenté à l'Assemblée Générale Annuelle de Québec-Océan à Rimouski, Canada.

Ce travail est une contribution aux programmes scientifiques d'ArcticNet (Université Laval), un réseau de centres d'excellence du Canada pour l'étude des impacts des changements climatiques en Arctique canadien, de l'unité mixte internationale Takuvik qui est une association entre l'Université Laval et le Centre National de Recherche Scientifique (CNRS – France) qui vise à mieux comprendre l'impact des perturbations environnementales actuelles d'origine climatique et anthropique, sur les écosystèmes et les géosystèmes arctiques, marins et terrestres, et prend part aussi au programme de recherche de l'association des scientifiques en Océanographie du Québec, Québec-Océan.

L'étudiante en Post-Doctorat Christiane Dufresne a permis la mise en place des forçages physiques de lumière en fonction des prévisions de concentration en glace de mer venant de la version de NEMO d'Environnement Canada, CREG12. Les forçages en nutriments dans le golf d'Amundsen ont été fournis par le Professeur Jean-Éric Tremblay. J'ai réalisé l'ajout de métazoaires réalistes ainsi que du trait fonctionnel de la diapause, l'analyse des résultats et la mise en forme de ceux-ci. J'ai pu bénéficier de la supervision de mon directeur de recherche, le Professeur adjoint Frédéric Maps, lors de la rédaction de la première version du manuscrit ainsi qu'à chaque étape de mes travaux de recherche.

1. Introduction générale

1.1. Le contexte Arctique

L'Arctique est la zone de la planète la plus affectée en intensité et en rapidité par les changements climatiques (Bennett et al. 2015). Ceux-ci ont pour principale origine les activités industrielles et agricoles humaines qui ont atteint une telle influence sur notre planète que nous avons basculé depuis le siècle dernier dans une nouvelle ère, l'anthropocène (Waters et al. 2016). Les changements climatiques se traduisent notamment par une augmentation de température de l'atmosphère et de l'océan. Cette augmentation est au moins trois fois plus rapide et elle atteint des niveaux trois ou quatre fois plus élevés en Arctique que la moyenne du reste du monde (Holland and Bitz 2003; Stocker et al. 2013). Ce phénomène est qualifié d'amplification arctique (Walsh et al. 2008; Johannessen and Miles 2011; Polyakov et al. 2013). Ainsi dans ce contexte de changement climatique, il est primordial d'améliorer notre compréhension du système arctique afin de pouvoir mieux prévoir les futures implications que ces changements pourront avoir à l'échelle de l'Arctique ainsi qu'à l'échelle mondiale.

L'impact le plus immédiat et visible des changements dramatiques en cours s'observe sur la dynamique de la glace de mer arctique. On observe un recul accéléré et très net de la surface et de l'épaisseur de la glace de mer multi-annuelle qui survivait habituellement à plusieurs cycles saisonniers annuels (Lindsay et al. 2009; Comiso 2012; Hinzman et al. 2013). Certains modèles indiquent qu'il est très probable que l'Océan Arctique soit libre de glace en été dès 2030 (Overland and Wang 2013; Wang and Overland 2012). Avec cette tendance pluriannuelle de réduction du couvert de glace, on observe ainsi un retrait saisonnier des glaces de mer plus hâtif d'une année à l'autre. Ce retrait hâtif a des conséquences pour les écosystèmes sympagiques se développant directement dans la glace en réduisant le période pendant laquelle ces écosystèmes peuvent se développer. D'autre part, une réduction de l'épaisseur de la couche de glace, ainsi que de la couche de neige recouvrant cette glace, a été observé au fil des années. Cette réduction a des conséquences pour les écosystèmes pélagiques car ce sera l'épaisseur de la couche de glace, en association avec le couvert de neige, qui modulera la pénétration de la lumière vers les producteurs primaires. Finalement, la glace de mer module les processus de mélanges verticaux dans la colonne d'eau, s'interposant entre les forces atmosphériques au-dessus et les masses d'eau en dessous (Forest et al. 2011; Tremblay et al. 2011). Ainsi, elle a aussi un impact indirect sur l'accès aux nutriments provenant des profondeurs. La tension entre ces deux forçages physiques essentiels, la lumière et les nutriments, sont à la base du contrôle de la production primaire planctonique arctique.

1.2. Écosystèmes marins arctiques

La dynamique de l'initiation de la production primaire au printemps est définie par la disponibilité de la lumière. Celle-ci réapparaît au printemps pour devenir maximale et quasi-continue en été. En parallèle, pour les milieux pélagiques arctiques, c'est la faible quantité de nitrates disponibles dans la couche de surface en association avec l'action du zooplancton, qui limitera l'amplitude de la production dans le système (Brugel et al. 2009; Tremblay and Gagnon 2009; Tremblay et al. 2015a). Ces variations environnementales peuvent être modulées en fonction d'un gradient latitudinal, ainsi qu'en fonction du bassin étudié, qui influencent alors la dynamique saisonnière (phénologie) des communautés planctoniques arctiques (figure 1, Ardyna et al. 2011, 2014; Leu et al. 2011; Wassmann and Reigstad 2011).

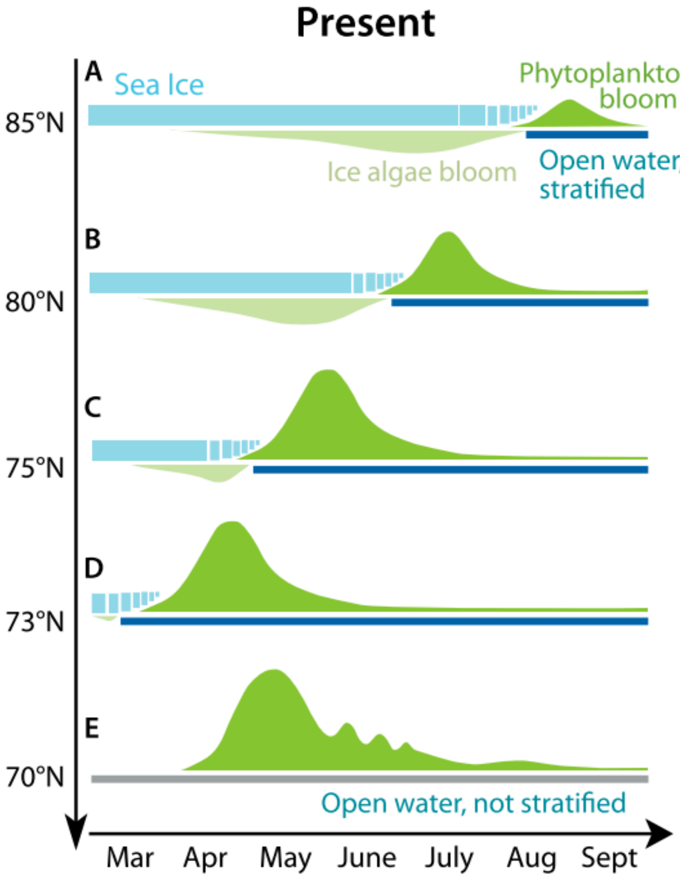

Figure 1 : Différente phénologies phytoplanctoniques le long d'un gradient latitudinal en Arctique (Wassmann and Reigstad 2011).

À la base de tout écosystème marin, le phytoplancton est constitué de cellules photosynthétiques (figure 2). Celles-ci transforment la matière inorganique, composée des nutriments (i.e. nitrates, silicates, fer, calcium) et du CO_2 dissous, en matière organique via la photosynthèse. Ces cellules sont ensuite consommées par le zooplancton, un groupe hétéroclite très diversifié composé d'êtres unicellulaires et métazoaires de petites tailles (inférieurs à 1 cm) qui forment un point de concentration et de transfert de la matière organique vers l'ensemble des niveaux supérieurs des réseaux trophiques marins arctiques. Les assemblages de producteurs planctoniques sont composés d'espèces présentant différentes stratégies de survies adaptées à ces environnements variables et extrêmes. À la base de tout écosystème pélagique, les espèces phytoplanctoniques doivent développer des compromis entre leurs tailles, les nutriments qu'elles peuvent assimiler ainsi que la quantité de lumière dont elles ont besoin pour faire de la photosynthèse (Martin et al. 2010). Ces compromis se sont mis en place afin que ces espèces puissent occuper différentes niches écologiques leur permettant de se développer à des moments ou à des endroits différents dans les couches supérieures de la colonne d’eau.

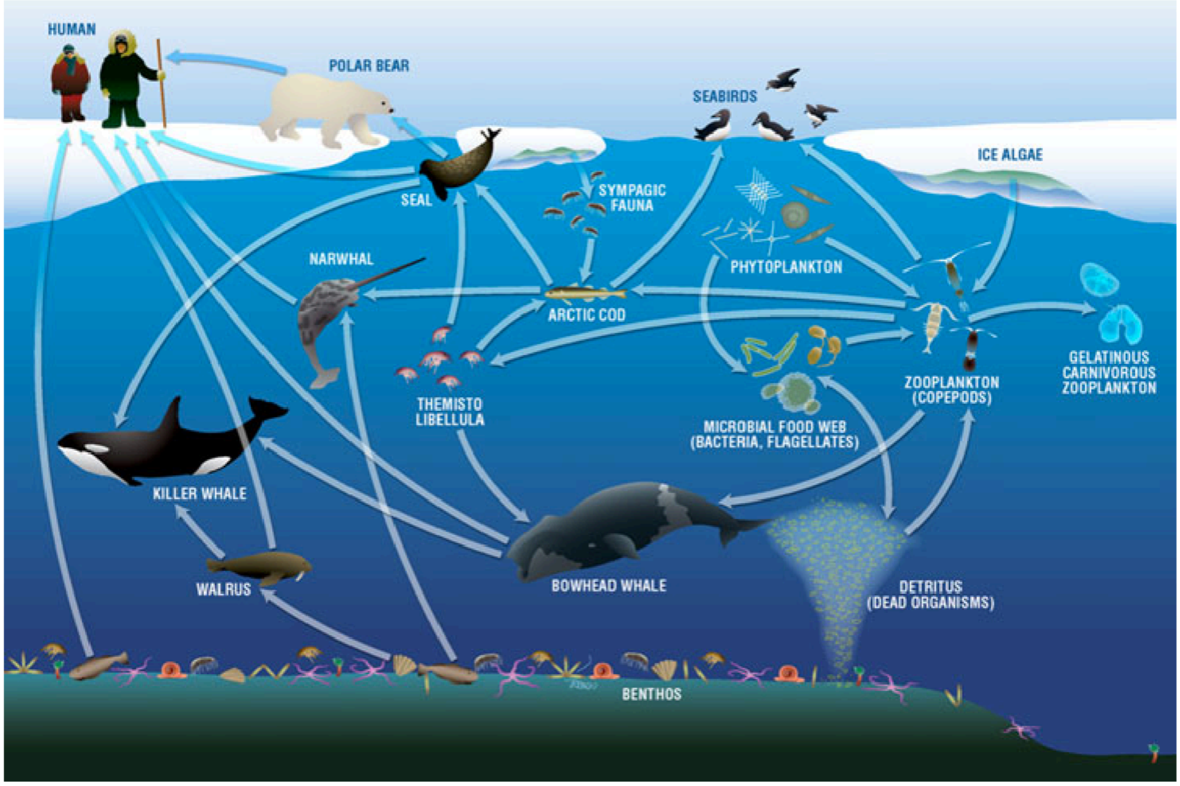

Figure 2 : Schéma du réseau trophique retrouvé en Arctique (Darnis et al. 2012).

1.3. Le phytoplancton arctique

Au printemps, lorsque la concentration en nutriments est relativement élevée et que la lumière réapparait, les grandes cellules eucaryotes telles que les espèces de diatomées *Thalassiosira sp.*, *Chaetoceros sp.* ainsi que la prymnesiophycée *Phaeocystis pouchetii* dominent les communautés phytoplanctoniques (Booth et al. 2002; Wassmann, Ratkova, and Reigstad 2005; Martin et al. 2010). Celles-ci vont être les plus efficaces à se développer en présence de lumière et de concentrations en nutriments relativement élevées du fait de leurs capacités à absorber et stocker ces nutriments dans leurs grandes vacuoles

(Sunda and Hardison 2010). Plus tard dans la saison, leur croissance entraîne une pénurie de nutriments dans la couche de surface. Il y aura alors la dominance d'un seul écotype de prasinophyte *Micromonas* dans les couches supérieures de la colonne d'eau (Balzano et al. 2012) jusqu'en automne pour ensuite être remplacé par un autre écotype de prasinophyte *Bathycoccus* qui dominera la communauté phytoplanctonique de surface jusqu'à la fin de l'hiver (Joli et al. 2017). Les espèces retrouvées à ces profondeurs semblent survivre à de très faibles concentrations en nutriments (aux alentours de 2, 0.1, 1 et 10 µmol kg $^{-1}$ respectivement pour le nitrate, le nitrite, l'ammonium et le silicate) grâce à leurs faibles ratios surface/volume (Martini et al. 2016). En parallèle, dans certaines régions et dès la fin-juin (d'après le modèle développé par Martin, Dumont, and Tremblay 2013) cette pénurie en nutriments déplace les communautés phytoplanctoniques vers des profondeurs proches de la nutricline (entre 25 – 35 m pour l'ensemble de l'Arctique). Certaines espèces vont suivre la nutricline et présenter une photo-acclimatation, leur permettant de compenser la faible luminosité présente à ces profondeurs (Palmer et al. 2011; Martin, Dumont, and Tremblay 2013). Il y aura la formation d'un maximum de chlorophylle sub-superficielle (MCS), où le phytoplancton présente un compromis entre accessibilité en nutriments et lumière.

Semblable à la dynamique des assemblages phytoplanctoniques, les communautés zooplanctoniques vont elles aussi varier en fonction des saisons et présenter une multitude d'adaptations à un milieu fortement saisonnier.

1.4. Le zooplancton arctique

Tout comme pour le phytoplancton, le zooplancton doit trouver un compromis entre la taille de l'individu, son activité métabolique, son alimentation (herbivore, carnivore, omnivore, détritivore) ainsi que son type de prédation. Chaque stratégie résultant de ces compromis leur permet ainsi d'occuper des niches écologiques différentes. Dans ce projet de maîtrise nous nous focaliserons sur les espèces de copépodes arctique. Ceux-ci peuvent représenter jusqu'à 80% de la biomasse zooplanctonique arctique (Falk-Petersen et al. 2009; Kosobokova and Hopcroft 2010). Les petites espèces de copépodes telles que *Pseudocalanus spp.* et *Microcalanus pygmaeus* survivent toute l'année en se nourrissant de particules organiques diverses (Darnis and Fortier 2014). À l'interface entre ces petites espèces (inférieures à 1mm) actives toute l'année et les grosses espèces (supérieures à 2 mm) de copépodes riches en lipides se trouve l'espèce de taille moyenne (entre 1 – 2 mm) *Metridia longa*. Celle-ci accumule une petite réserve de lipides lui permettant de palier à de courtes périodes de disette mais reste toutefois active toute l'année en se nourrissant de façon omnivore sur la matière particulaire en suspension (Darnis and Fortier 2014). Elle peut aussi à l'occasion se nourrir d'œufs flottants chargés de lipides de *Calanus hyperboreus* (Conover & Huntley 1991; Darnis et al. 2012; Dufour et al. 2016). Au sommet du spectre de taille des copépodes arctiques on retrouve des espèces qui, afin de survive à la forte saisonnalité de la disponibilité de leur nourriture, accumulent de grandes réserves lipidiques pendant l'été afin de combler leurs besoins énergétiques lorsque les producteurs primaires se font rares plus tard dans l'année. Ces espèces de copépodes, représentées essentiellement par le genre *Calanus*, peuvent avoir plus de 50% de leur biomasse sous forme de lipides (Falk-Petersen et al. 2009) eux-mêmes pouvant être composés jusqu'à 90% d'ester de cire qui sont la forme la plus énergétique de lipides (Kattner et al. 2007; Kattner and Wilhelm 2009). Via cette accumulation de lipides, les niveaux trophiques supérieurs se nourrissant de ces copépodes ont alors accès toute l'année, aux profondeurs de diapause de ces copépodes, à la forte production primaire se déroulant pendant la courte fenêtre optimale de production primaire arctique.

1.5. Le métabolisme des lipides

L'hypothèse selon laquelle les copépodes, dont le métabolisme se base sur l'utilisation des lipides, sont adaptés à des environnements très variables ou à de longs épisodes de famine a été avancée par les recherche de Mayzaud & Conover (1988). Au cours de leurs expériences, ils ont utilisé différents rapports élémentaires et ont déterminé que la petite espèce (inférieure à 1 mm) cosmopolite de copépode *Acartia tonsa*, ne présentant pas de phase dormante, a un catabolisme protéique. À l'inverse, lors d'une période de famine, l'espèce de latitudes moyennes boréales *Calanus finmarchicus,* qui présente une phase dormante dans son développement, aurait un catabolisme à base de lipides. Cette étude désigne les lipides comme un mécanisme d'accumulation de l'énergie à un faible coût et serait une adaptation aux événements de famine récurent. Ils associent les espèces zooplanctonique utilisant des lipides avec un habitat profond et/ou arctique, tandis que les espèces zooplanctoniques utilisant des protéines seraient plutôt associées à la surface et aux latitudes tempérées/tropicales. Néanmoins, d'autres études ont montré que ces « types » dépendent plutôt de l'espèce étudiée (Ohman et al. 1998; Mayzaud 1976) ainsi que de la taille de celle-ci (Talmy et al. 2014).

La synthèse des lipides dépend aussi de la phase de développement de l'individu étudié ainsi que de la composition biochimique de ses proies (Conover and Huntley 1991; Anderson 1992; Kattner et al. 2007; Mitra, Flynn, and Fasham 2007; Meunier et al. 2016; Flynn and Mitra 2016) . Les mesures d'action dynamique spécifique (SDA) des stades copepodites et des femelles de *C. finmarchicus* révèlent en effet des différences dans les voies métaboliques suivies par l'énergie acquise de leurs proies (Thor 2002). Une fois le coût de maintenance couvert, les femelles synthétisent les protéines nécessaires à la production d'œufs tandis que les copepodites synthétisent et accumulent des réserves de lipides afin de pouvoir compléter leur cycle de développement. Ainsi, l'accumulation de lipides chez certaines espèces de copépodes sera une des conditions fondamentales à la mise en place d'une stratégie de cycle de vie leur permettant d'éviter les conditions environnementales défavorables : la diapause.

La diapause est un trait que l'on peut retrouver parmi de nombreuses espèces adaptées à des environnements présentant une forte variation saisonnière (Dahms 1995; Wang et al. 2016). Avant que les conditions environnementales ne se détériorent, les espèces de copépodes dotées de ce trait vont cesser de se nourrir, migrer en profondeur et ralentir leur métabolisme (passer en dormance) jusqu'à ce que les conditions environnementales redeviennent favorables. En Arctique, ce sont essentiellement des espèces du genre *Calanus,* riche en lipides qui présentent ce trait (Falk-Petersen et al. 2009). Ces auteurs ont trouvé que pour différentes espèces de *Calanus* arctique, présentant différentes durées de vie ainsi que différents stades de développement, chaque cohorte présentant la même taille passent en diapause au même moment (Falk-Petersen et al. 2009). Ceci suggère que la taille d'un individu impose une quantité spécifique de lipides afin que celui-ci puisse survivre pendant la période de famine prolongée (e.g. Maps et al. 2014).

Les diverses stratégies présentées précédemment, que ce soit chez le phytoplancton ou le zooplancton, permettent à chaque espèce de survivre aux variations extrêmes de l'environnement ainsi que de la disponibilité en nutriments et en nourriture propre aux écosystèmes marins Arctique. En parallèle, chacune de ces stratégies va avoir des spécificités qui vont apporter des variations en nutriment et en matière organique dans ce même environnement (par ex. pénurie d'azote dans les couches de surfaces due à la production primaire, forte production de particules organiques). C'est en étudiant l'association de ces différentes adaptations et stratégies de cycle de vie au niveau des communautés phytoplanctoniques et zooplanctoniques que l'on peut améliorer notre compréhension de l'écosystèmes pélagiques arctiques, de la dynamique de ses populations et mieux comprendre leurs cycles biogéochimiques.

1.6. Problématique et objectifs de recherche

Le but pratique de cette étude est de mettre en place le trait fonctionnel de la diapause dans un modèle biogéochimique dans un contexte arctique. Ce trait étant central dans la dynamique des communautés planctoniques arctique, sa prise en compte devrait nous permettre de mieux les caractériser grâce à la modélisation numérique. Les modèles numériques permettent de comprendre la structure et le fonctionnement du système que l'on veut étudier en synthétisant une grande quantité de données et de connaissance sur les mécanismes du système. Les modèles biogéochimiques sont des modèles numériques s'intéressant aux relations trophiques entre le phytoplancton et le zooplancton et leur environnement, permettant ainsi d'estimer quantitativement les flux de divers éléments essentiels (carbone, azote, oxygène, etc.). Dans ces modèles, le système est simplifié en quelques compartiments représentant les grands groupes organisationnels que sont les nutriments, le phytoplancton, le zooplancton et les détritus (NPZD). Durant la dernière décennie il y a eu l'apparition de modèles NPZD dits émergents. Ces modèles s'intéressent aux mécanismes de mise en place et de successions des communautés modélisées. Ceux-ci utilisent une approche basée sur l'utilisation de traits fonctionnels associés à des relations allométriques entre diverses tailles et métabolismes (Size Spectrum Models, Blanchard et al. 2017). L'émergence des communautés se fait en fonction de la capacité des espèces numériques à survivre au milieu physique qui leur est présenté.

Dans la plupart des modèles NPZD, l'environnement (nutriments, lumière, la température et la salinité) régule la phénologie (dynamique saisonnière) du phytoplancton alors que le zooplancton ne constitue qu'un terme de fermeture du système modulant l'abondance du phytoplancton (e.g. Riley 1946, Anderson & Gentleman, 2012). Toutefois, le zooplancton peut présenter un fort contrôle descendant (*Top-down*) sur les communautés phytoplanctoniques (Olli et al. 2007; Banse 2011; Sommer et al. 2011; Menden-Deuer and Kiørboe 2016). De plus, certains comportements, comme la migration saisonnière ou journalière, présents chez certaines espèces zooplanctoniques semblent jouer un rôle clé dans la dynamique des échanges de matière et d'énergie des écosystèmes marins (Jónasdóttir et al. 2015; Hansen and Visser 2016; Steinberg and Landry 2017). Dès lors, on peut supposer que les interactions complexes entre les espèces phytoplanctoniques et zooplanctoniques adaptées à ce milieu unique qu'est l'Arctique influencent probablement les successions spécifiques, les assemblages, les fonctions (ex : export de carbone) et l'organisation spatiale (ex : MCS) des communautés planctoniques.

La diapause étant l'un des mécanismes clefs dans la survie des espèces représentant la majorité de la biomasse zooplanctonique arctique, on peut s'attendre à ce que ce trait ait un impact majeur sur la phénologie phytoplanctonique et zooplanctonique arctique. Ce travail de maîtrise tentera d'ajouter ce trait fonctionnel au modèle biogéochimique DARWIN. Nous essayerons de déterminer l'impact que devrait avoir une meilleure représentation du zooplancton métazoaire arctique dans le modèle DARWIN sur la reproduction de la dynamique des assemblages planctoniques arctiques. Pour ce faire il sera nécessaire d'adapter la représentation du zooplancton retrouvée actuellement dans DARWIN afin qu'elle puisse correspondre à des communautés zooplanctoniques arctiques.

2. Diapause as functional trait of a biogeochemical model of an Arctic pelagic ecosystem.

2.1. Résumé

Certaines espèces de zooplanctons métazoaires arctiques ont développés un mécanisme leur permettant de tirer profit de la production primaire pulsative présente en Arctique tout en évitant des conditions défavorables à leur développement : la diapause. En accumulant des réserves lipidiques sur une période limité, migrant en profondeur et modulant leur métabolisme, ces espèces font le pont entre deux saison productives. Pour ces espèces représentant la majorité de la biomasse zooplanctonique en Arctique, le trait de la diapause devrait avoir de fortes implications tant pour la dynamique des populations que pour les flux d'éléments tels que le carbone et l'azote présents en Arctique. Cette étude est la première à prendre en compte ce trait fonctionnel afin d'en étudier l'impact sur la dynamique d'espèces planctoniques fonctionnelles arctiques au sein d'un modèle biogéochimique. Nos résultats démontrent la faisabilité de la mise en place du trait de la diapause dans un modèle eulérien.

2.2.Abstract

Many Arctic mesozooplankton species graze intensely on the short pulse of primary production in spring to accumulate lipids in preparation for an extended dormant period at depth, the diapause (no feeding, reduced metabolism and activity). Diapause is a key adaptation of copepod species of the *Calanus* genera that enables individuals to survive the harsh autumn and winter months at depth, before migrating again to favorable surface conditions in spring. The resulting conversion of the short-lived Arctic primary production into massive lipid stocks and its displacement for extended periods of time to the relative security of the depths is central to the trophic dynamic of the Arctic Ocean. However, the diapause dynamics is still overlooked in numerical models. In order to improve our understanding of the effects of diapause on Arctic pelagic ecosystems, we implemented it as a functional trait of mesozooplankton numerical species in the DARWIN model that simulates emerging planktonic communities in response to environmental forcing. We assumed that the control of diapause in mesozooplankton species involves the metabolism of lipids. We used the C to N elemental ratio (C:N) as a proxy of the lipid content of numerical mesozooplankton species in the model. Since lipids do not contain nitrogen, the more lipids zooplankton accumulates, the higher the C:N ratio. Initiation and termination of diapause in the model depended on C:N ratio thresholds as a proxy of the species condition. Our results demonstrate the feasibility of implementing the diapause trait into an Eulerian model. With our approach, we could obtain one metazoan species that exhibited a diapause pattern comparable to observations. Then we explored the possible impacts that this trait could have in biogeochemical models, such as trophic cascades inducing changes in the phenology of both microzooplankton and phytoplankton functional species.

2.3. Introduction

Despite being oligotrophic during a major part of the year, the Arctic is characterized by an acute pulsatile primary production (Tremblay and Gagnon 2009; Arrigo et al. 2012; Tremblay et al. 2012). This system has an environmental bottom-up control that regulates the intensity of the primary production (Tremblay et al. 2015a) as well as the main marine communities' dynamics. Even before the spring retreat of the sea ice, some locations in the Arctic can exhibit primary production that starts within and under the ice (Tremblay et al. 2012; Ji, Jin, and Varpe 2013; Leu et al. 2015). When sea ice melts, the ice algae that developed within the ice will sink, forming a significant flux of biomass (as high as 57% of the total primary production in some areas of the central Arctic's Ocean multi-year ice pack, Gosselin et al. 1997) into the water column via the zooplankton grazing (Michel et al. 1996) and also towards the depth and the benthic communities (Boetius et al. 2013). Shortly after the retreat of the ice, we usually observe a bloom of centric diatoms that will last until the depletion of surface nutrients. Later, when the surface water (from 0 to 25 m) nutrients will be depleted we can see in some regions the occurrence of a Subsurface Chlorophyll Maximum (SCM) towards the nutricline (Martin et al. 2010; Martin, et al. 2013). Finally, the primary production slows down as light decreases and sea-ice starts to form. Throughout the year there is a succession of phytoplankton communities dominated by different species (Martin et al. 2010) of which dynamic can vary according to the latitude (Leu et al. 2011). Furthermore, this community evolution is characterized by a transition from Diatoms dominated new primary production to a *Micromonas*/micro-zooplankton dominated recycled/heterotrophic production (see Wassmann, 2011 its figure 6a). Then, by being at the heart of the carbon biogeochemical cycle, having accurate (or at least more realistic) estimation of the biological pump related to this community dynamic in the Arctic ocean is essential in order to set relevant carbon release threshold policy.

With such a strong bottom-up control, the top-down control that the secondary producers might have on the biogeochemistry and the dynamic of these pelagic ecosystems has usually been overlooked, even though it might be of relevance (Buitenhuis et al. 2006; Olli et al. 2007; Mariani et al. 2013; Friedland et al. 2016; Menden-Deuer and Kiørboe 2016). From a population dynamics point of view, zooplankton can have a major role in grazing the primary producers biomass as well as influencing the phytoplankton community succession (Olli et al. 2007; Mariani et al. 2013; Friedland et al. 2016). Additionally, the diverse migration patterns (diel or seasonal), the “sloppy” feeding as well as the excretion of mesozooplankton can have a significant role in the biogeochemical fluxes (Buitenhuis et al. 2006; Jónasdóttir et al. 2015; Menden-Deuer and Kiørboe 2016).

Representing up to 80% of the mesozooplankton biomass, copepods are the most representative zooplankton type and hence are the major secondary producers in the world (Turner 2004). In the Arctic, up to 90% of this biomass is composed by a few species (*Calanus hyperboreus*, *Calanus glacialis*, *Calanus finmarchicus*, *Metridia longas* , Falk-Petersen et al. 2009). Most of these species have developed a behaviour specific to extremely variable environments, allowing them to pursue their ontogenic development while avoiding unfavorable environmental conditions: the diapause.

The diapause, performed mostly by *Calanus* copepods in the Arctic, can be found in every highly seasonal environment (Poles and upwelling area). It allows them to avoid situations that would impede growth, reproduction or even survival (“[...]to bridge periods of environmental harshness.”, Dahms 1995; Falk-Petersen et al. 2009). Such situations would lead to environments or periods of time exhibiting temperature/salinity that are out of their preferred range (Hirche 1987; Conover and Huntley 1991; Gradinger and Schnack-Schiel 1998). Since these situations occur in winter in high-latitudes it is often said that individuals in diapause are over-wintering (but we can also find species of copepods over-summering at low latitudes Wang et al. 2016). The individuals are dormant at certain depths during the bad season and rely on their lipid reserves. As soon as the pulsed productive season starts, they go at the surface and feed on primary producers and the micro-zooplankton. It is at that time that they accumulate lipids (either directly from their prey or by biosynthesizing them, Kattner et al. 2007) mostly in the form of esters. These species will go at depth at the end of the bloom, or even before the end of the bloom for some developmental stages, reduce their metabolism and wait until the next productive season (Darnis and Fortier 2014). This allows the transfer of a pulsed primary production to a year-long consumption by the higher trophic levels. This process is possible thanks to the accumulation of energy in the form of lipid reserves. Because no single environmental parameter could explain the diapause dynamic (yet), it is the use of these lipids reserves that has been at the focus of most of the research studying diapausing species (Johnson et al. 2008; Maps et al. 2011; Maps, Record, and Pershing 2014).

Most of the work done on the diapause are trying to understand how this trait is regulated (Johnson et al. 2008; Tarrant et al. 2016) and how it can explain the distribution and phenology of the species doing it (Maps, Record, and Pershing 2014). But despite all the work done on understanding and reproducing the diapause trait, no models (to our knowledge) studied its potential impact on the environment and the communities living in it.

This is surprising since, estimation from field data have shown that the flux of carbon associated with the diapause (lipid pump, Jónasdóttir et al. 2015) is comparable to the flux of carbon related to the sink of particulate organic matter (Darnis and Fortier 2012; Jónasdóttir et al. 2015). Then, this key behavior, or functional trait, should have strong implications on the phenology and the biogeochemistry of the whole Arctic pelagic ecosystem but have never been taken into account into the currents models that tries to understand the highly variable Arctic environment. This lack of representation of the diapause and especially the accumulation of lipids related to it into biogeochemical models have been criticized in several studies (Mitra et al. 2014; Steinberg and Landry 2017; Jónasdóttir et al. 2015; Menden-Deuer and Kiørboe 2016).

Being at the heart of the understanding of the nutrient flux within an ecosystem, the biogeochemical models are key tools in the process of policy making and regulations (Bashkin and Demidova 2008). It is then always necessary to improve their representation of the natural processes that might influence the flux of critical elements such as carbon. Each biogeochemical model has its own advantages and drawbacks according to their assumptions and structures. The biology of these model is usually represented by a NPZD model (nutrients, phytoplankton, zooplankton and detritus). One drawback of such models is that they usually tend to oversimplify the zooplankton compartment, using it only as an exit terms for the phytoplankton. Another drawback in such model is the fact that the grazing pressure on the phytoplankton is usually constant. This would not be representative of the Arctic pelagic ecosystem since most of its mesozooplankton goes into diapause which modulate their pressure over their planktonic preys throughout the year.

The objective of this research is twofold. This is an attempt to add the functional trait of diapause that has never been integrated yet into an emergent biogeochemical model. This will give us a better insight on the evolutionary advantage that this trait can have for mesozooplankton in the Arctic ecosystem. It will also allow us to investigate how that trait would impact the other species of the model. Since diapause is a key trait for the Arctic pelagic ecosystem, we are expecting to improve our representation of that ecosystem. Finally, this will be a proof of concept for future studies advocating to take into account the developmental trait of diapause. To achieve this objective, we needed to follow few simple assumptions regarding the functional trait of diapause itself that are described below.

2.4. Model description

2.4.1. Diapause implementation

Diapause fits the functional trait definition since this life-cycle strategy involves ontogenetic, physiological and behavioral processes measurable at an individual level (Violle et al. 2007. Moreover, diapause is both a “response” trait that results from the individual’s response to external forcing and an “effect” trait that have a major impact on ecosystem properties (Hébert, Beisner, & Maranger 2016a; 2016b). We considered two major categories of biological processes to implement this trait in the model, i.e. the lipid metabolism and the ontogenetic vertical migration

To enable the survival of the diapausing species, the diapause strategy relies on the presence of large energy reserves and mechanisms to use this capital parsimoniously. The former condition is met thanks to the energy-rich lipids that are the staple of marine food webs. The diapause trait is expressed in different ways among mesozooplanktonic species, but a common attribute of all those relying on this strategy during their life cycle is their high lipid content. Lipids in calanoïd copepods that typically dominates the mesozooplankton assemblages of seasonal marine ecosystems can reach 80% of their dry weight in some species and places, with a typical value around 50% (Lee, Hagen, and Kattner 2006). Since lipids are rich in carbon but devoid of nitrogen, variation of the atomic ratio of carbon to nitrogen (C:N) has been used for decades as an indicator of the condition of zooplankton and of its primary source of metabolism among protein, carbohydrates and lipids (e.g. Mayzaud 1976; Anderson 1992; Thor 2002; Alcaraz et al. 2010). A high C:N ratio in zooplankton tissues means that individuals tend to accumulate a lot of lipid, whereas a low C:N closer to the Redfield ratio indicates a metabolism in balance with the stoichiometric composition of its food. Hence, we will rely on the atomic C:N ratio of zooplankton biomass for implementing the control of the diapause trait in numerical species of the mesozooplankton functional group.

2.4.2. Respiration and excretion

Respiration is the expression of the individual's metabolic demand that can vary substantially according to its level of activity, its physiological state and its ontogeny. The second condition to emulate the diapause strategy requires a reduction in metabolic demand during diapause. Maps et al. (2014) showed that the metabolism of several calanoïd copepod species was reduced from one third to one fifth of its level during the active phase of their life cycle. Hence, we assumed that the respiration rate (carbon loss) of mesozooplankton species was reduced by a factor of five during diapause.

Excretion is also related to the metabolism of mesozooplankton. However, excretion of nitrogen is essentially controlled by the stoichiometry of its preys and the balance between the anabolic and catabolic activities of the individual (Thor 2000; 2002). In particular, for an individual to be able to accumulate large quantities of carbon that will be incorporated into lipids and increase its C:N ratio, and excess of nitrogen has to be evacuated. Moreover, the atomic turnover rate of carbon and nitrogen has to be different too, since carbon will be stored into lipids, while nitrogen will continue to be (essentially) a key element of proteins that are rapidly synthesized and recycled within cells (Bamstedt and Tande 1985). As a results, excretion rates measured are not in stoichiometric balance with respiration rates, and this decoupling will be the key mechanism chosen to allow simulate mesozooplankton species to very their C:N ratios. Moreover, since the reduced metabolism of diapausing mesozooplankton is sustained by the mobilization of lipid stores, nitrogen excretion is extremely reduced or too low to be measured in individuals sampled *in situ* (e.g. Tande, 1982). Hence, we assumed that excretion was null during diapause.

2.4.3. Ontogenic vertical migration

The diapause trait is also characterized by ontogenetic migration towards the relative security of depth. Copepod species that enter diapause at a late development stage migrate before winter well below the deepening vertical mixed layer to reach depth where mortality by visual predation is drastically reduced (Heath et al. 1999; 2004). Here we use the vertical distribution observed by Darnis and Fortier (2014) in the Gulf of Amundsen during winter and assumed that diapausing mesozooplanktonic species are spread around a target depth z_0 of 300 m for the diapausing stage and 15 m for the active stage. The corresponding eulerian state variable present a vertical migration speed that follows a hyperbolic tangent form using a chosen speed attenuation index α (Zakardjian et al. 1999; Maps et al. 2011). That speed was zero at depth z_0:

$$W_i(z) = W_i^{max} \tanh(\alpha\,(z - z0_i)) \tag{1}$$

$$W_i^{max} = 2\left(\frac{(3\ B_i)}{(4\ \pi)}\right)^{\frac{1}{3}} 10^{-6} \,/\, W^{fac} \tag{2}$$

with W_i^{max} the maximum swimming speed of the functional species *i*, a scaling parameter, *z* the actual depth, $z0_i$ its target depth, B_i its biovolume and W^{fac} a scaling factor used to adjust the swimming speed W_i^{max} of the functional species *i.*

Maximum vertical speed of migrating mesozooplankton is typically of a few body lengths per second. Hence, we parameterized eq(1) so that the maximum vertical speed of each species was proportional to the equivalent spherical diameter generated by the model, with a maximum of 2.08×10^{-4} m s^{-1} (c.a. 18 m d^{-1}) to ensure numerical stability.

2.4.4. Model modification

We implemented mesozooplanktonic functional groups and their diapause functional trait in the DARWIN ecosystem module (Follows et al. 2007; Ward et al. 2012; Dutkiewicz et al. 2015) that was coupled to the MITgcm model (Massachusetts Institute of Technology general circulation model). We forced the model with Arctic data from the Amundsen Gulf (see below). The emergent biogeochemical DARWIN model couples the functional trait approach with structured size classes (Ward et al. 2012; 2014). It generates many functional groups (j) defined by a unique set of traits (nutrient affinities, trophic interactions, metabolic rates, etc.) and parameters, and create within these groups several numerical species (i) that are spread along a group-specific size range. These species then respond to their simulated environment and interact with one another. The species that are the most fit will thrive, whereas others will not. This is how, after some years of simulation, a community of locally adapted numerical species emerges.

2.4.4.1. Implementing metazoans

We used the same general model setup than Ward et al. (2012a), and we direct the reader to the online supplemental material of their paper for further details on the original equations and parameters values or the online supplemental material from our paper for further details on our implementation. A fundamental feature of the model is the prevalence of the allometric relationship in most physiological rates:

$$p = a\,M^{b} \tag{3}$$

where p is the rate per unit of time, a is a scaling factor, M a measure of size (often the biovolume or the carbon content) and b the allometric exponent lower than unity. In DARWIN, a is the same for a whole functional group and can vary between groups.

Once all the physiological rates are calculated, the biomass in each depth layers in either carbon and nitrogen was calculated. For mesozooplankton, the following equation were used (notwithstanding the upward and downward flux from the other depth layers):

$$\frac{d[Mc_i]}{dt} = -m_i[Mc_i] - R_i[Mc_i] + \sum_{j=1}^{J}[Mc_i]G_{i,j}\lambda_{i,j} \tag{4}$$

$$\frac{d[Mn_i]}{dt} = -m_i[Mn_i] - E_{N,i}[Mn_i] + \sum_{j=1}^{J}[Mn_i]G_{i,j}\lambda_{i,j} \tag{5}$$

with $[Mc_i]$ the concentration in mmol of carbon of mesozooplankton i, $[Mn_i]$ the concentration in mmol of nitrogen of mesozooplankton i, m_i the association of linear (mz_a^1) and density-dependent mortality (mz_a^2), $G_{i,j}$ the grazing rate function of G_i^{max} and kg_i^{prey}(table1, see Ward et al. 2012a), $\lambda_{i,j}$ the assimilation efficiency (ranging from 0.7 to 0.8, depending on the prey size preference) of mesozooplankton *i* toward the prey *j* from all its prey range *J*, R_i its respiration rate and $E_{N,i}$ its excretion rate.

For mesozooplankton, most of the size-dependent relationships could not be extrapolated from the microzooplankton to the mesozooplankton. There are fundamental biological differences between unicellular and metazoan creatures, especially concerning feeding and metabolism. Hence, we added a copepod-like functional group with allometric relationships representative of metazoans (Fig. 3). By doing so, we aimed to reproduce realistic mesozooplankton metabolic rates. We were looking for processes comparable to what has been observed in the field. Then, to be considered realistic, these metabolic rates should be within the range of metabolic rates measured for species from the study area. For a numerical species to have a diapause considered as realistic, it should exhibit a migration pattern and phenology similar to homologous species in the field.

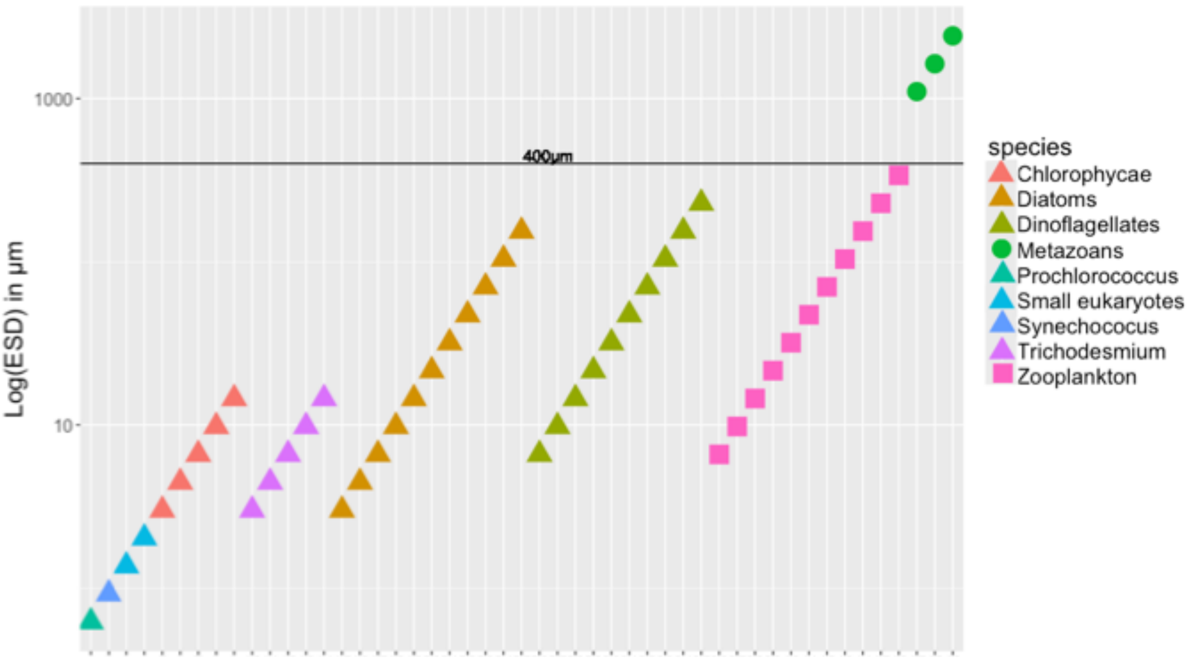

Figure 3: Functional groups, composed by their functional species, spread along their size range in ESD (Estimated Spherical Diameter in µm). Each color represents a different functional group. Triangles, scares and plain circles represents species in the phytoplankton, zooplankton and mesozooplankton compartment, respectively. The black line indicates the size limit above which we considered the species as metazoan species.

Excretion parameters required for the mesozooplankton functional group were computed from the dataset provided by Vanni and McIntyre (2016) (Table 1). The relationship obtained with all pelagic zooplankton species pooled together was driven by some very high excretion rates, in particular those of *Cladocerans* that have excretion rates approximately seven times higher than those of copepods (Vanni and McIntyre 2016). Hence, while remaining within the range provided, we had to tune down the scaling factor *a* for excretion to 0.09 mmol N mmol C^{-1} d^{-1} while keeping the same slope *b* of - 0.183. We further assumed that excretion occurred only when the metabolism was fueled by proteins, i.e. when mesozooplankton was actively feeding and not relying on its lipid reserves (Mayzaud and Conover 1988; Thor 2002). As a result, excretion was dependent on a lower ingestion threshold of 8.64×10^{-7} mmol C m^{-3} d^{-1}; it was null below (Table 1). The value of this low ingestion threshold has been calibrated to give a realistic time of lipid accumulation.

Respiration allometric relationship parameters were directly taken from the size-dependant relationships provided by Moloney and Field (1989). We calibrated the *a* (going from the original *a* value of 15 pgC to 12 pgC, table 1) in order to have realistic diapause patterns. The interplay between the active respiration rate and the excretion rate gave a realistic time of lipid accumulation during the growing season.

Finally, we adapted the trophic relationships. In the DARWIN configuration used by Ward et al. (2012a), the zooplankton grazing preferences (hereafter "palatability") were based on a ratio prey:predator of 0.1 (following Kiørboe and Jackson 2001). However Flynn and Mitra (2016) showed that the optimal palatability changes according to the type of zooplankton, with the unicellular ciliates having an optimal prey:predator ratio around 0.13, whereas copepods optimal palatability is an order of magnitude lower. Since the size range of the metazoan species we implemented overlapped the size range of copepods (900 µm to 2400 µm), we defined an optimal prey:predator ratio of 0.02, which remains within the range given by Flynn and Mitra (2016). An immediate consequence of this assumption was that most species of microzooplankton would be within the preferred target range for mesozooplankton species (Broglio et al. 2003; Mitra and Flynn 2005).

2.4.4.2. Control of diapause

Even though there is no consensus on the exact factors responsible for of the onset and the termination of the diapause period in mesozooplankton species, one plausible hypothesis that has not been falsified yet is the Lipid Accumulation Window (LAW) (Ohman et al. 1998; Johnson et al. 2008; Maps et al. 2011). The lipid accumulation window hypothesizes that lipid content should exceed an upper threshold for individuals to safely initiate diapause. Then, diapause would stop when a minimum lipid threshold is reached. Here, we used the C:N ratio as a proxy for lipid content of the species' biomass. As soon as the mesozooplankton species had reached a C:N ratio of 12, its biomass would transfer into diapause. The numerical implementation of diapause in the eulerian framework of the DARWIN model involved a mirror state variable that shared the same features and parameters, only modified for the diapause metabolism and behavior (reduced respiration, no excretion and ontogenetic migration to diapause depth; see sections above). Then, as soon as the C:N ratio would reach a lower limit of 6.5, the diapausing biomass would transfer into its active counterpart and resume an active metabolism and growth. These thresholds were based on typical C:N ratios of calanoïd copepods relying on diapause as a life-cycle strategy (Alcaraz et al. 2010a; Forest, et al. 2011). As in Ward et al. (2012a; 2014), the internal pools of carbon and nitrogen of each species are regulated following the quota approach (Droop 1968). Ward et al. (2012a) used fixed maximum and minimum nitrogen quota for the microzooplankton to tightly constrain the variations of the C:N ratio. However, in order to be able to reproduce the large variation of the C:N ratio required for the mesozooplankton functional group, we had to widen the range of possible nitrogen quota from the once used in Ward et al. (2012b)(Table 1).

It will be those thresholds, in addition with the interplay between respiration and excretion rate in association with the temperature, that will determine the timing of the diapause.

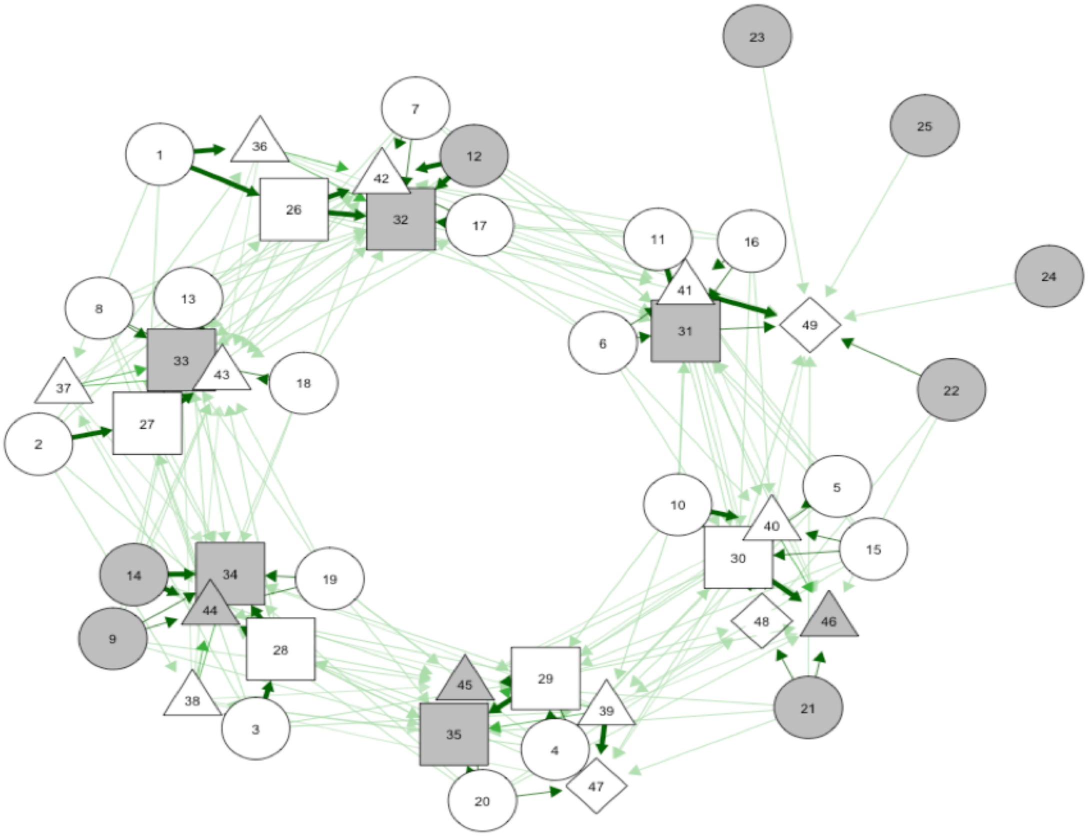

Figure 4 : Trophic network of our configuration of the model. The shape defines the main functional types: circle, square, triangle and diamond are for phytoplankton, mixotrophs, microzooplankton and mesozooplankton, respectively. The greyed functional species are the one that do not survives (total biomass below 1x10^{-15} mmol C m^{-2})

Table 1 : List of the functional metazoan parameters

Term	***Definition***	***Units***	***Values***			***Origin***
			M	***a***	***b***	
W_z^{max}	swimming speed scaling factor	unitless		6		chosen
Q_N^{max}	nitrogen maximum quota	mmol N m^{-3}		1.51×10^{-1}		chosen (Ward et al. 2012)
Q_N^{min}	nitrogen minimum quota	mmol N m^{-3}		4×10^{-2}		chosen (Ward et al. 2012)
$C{:}N^{high}$	High lipid threshold	mmol C mmol N^{-1}		12		chosen (Forest et al. 2010)
$C{:}N^{low}$	Low lipid threshold	mmol C mmol N^{-1}		6.5		chosen (Forest et al. 2010)
R	allometric respiration rate	mmol C pgC^{-1} d^{-1}	pgC	$1.20 \times 10^{+1}$ (mmol C d^{-1})	-0.306	calibrated from Moloney and Field 1989
E_N	allometric excretion rate	mmol N mmol C^{-1} d^{-1}	mmol C	9.03×10^{-2} (mmol N d^{-1})	-0.183	Extracted and calibrated from Vanni et al. 2016
G_C^{max}	maximal grazing	d^{-1}	pgC	$6.80 \times 10^{+1}$ (pgC d^{-1})	-0.316	Moloney and Field 1989
kg_C^{prey}	half-saturation grazing	mmol C m^{-3}	μm^3	5.94×10^{-1} (mmol C μm^3 m^{-3})	-0.14	Hansen et al. 1997
mz_a^1	linear mortality	mmol C d^{-1}		1×10^{-3}		Cadier 2016
mz_a^2	density-dependent mortality active phase	d^{-1}		8.64×10^{-2}		Ward et al. 2012
mz_d^2	density-dependent mortality diapause phase	d^{-1}		8.64×10^{-3}		chosen
α	speed attenuation index	unitless		7×10^{-3}		chosen (Zarkadjian et al. 1999)
G_C^{Th}	active nitrogen excretion grazing threshold	mmol C m^{-3} d^{-1}		8.64×10^{-7}		chosen

2.4.5. Model configuration

In addition to its evolutionary approach, the DARWIN model was already fully coupled with the global circulation model MITgcm. From there, to adapt it to the arctic context we needed to adapt its configuration and its forcing data to one location in the Arctic.

We apply our model to the Amundsen Gulf in the Western Canadian Arctic, with a maximum depth of 575 m in its center. The Amundsen Gulf, is open toward the Beaufort Sea that and the Mackenzie Shelf in the north that it connects it to the Canadian Arctic Archipelago (Figure 3).

The water column presents three water masses of different origin: a low salinity Polar-Mixed Layer (salinity < 31.6, 0-50m) resulting from the mix of melted sea-ice and sea-water, an intermediate Pacific Halocline (32.4 < salinity < 33.1, 50-200m) coming from the Pacific Ocean through the Bering strait and the deep, warmer and saltier Atlantic Waters (salinity > 34, > 200m) that flowed along the whole Arctic shelf (Carmack and Macdonald 2002).

Forcing data were taken from the CREG12 configuration of the NEMO ocean model developed by Environment Canada (Dupont et al. 2015, Dufresne et al. in prep) and *in situ* data collected during the Canadian Circumpolar Flaw Lead system mission (CFL) that occurred during a quasi-complete seasonal cycle between 2007 and 2008 (Tremblay et al. unpublished, Figure 3). Irradiance input from CREG12 followed the sea-dynamic present in the gulf with a fall formation in October, a consolidation in December and a breakup in May-June (Darnis and Fortier 2012). The coupled biophysical model needed a 4-year spin-up in order to reach a (quasi) steady state.

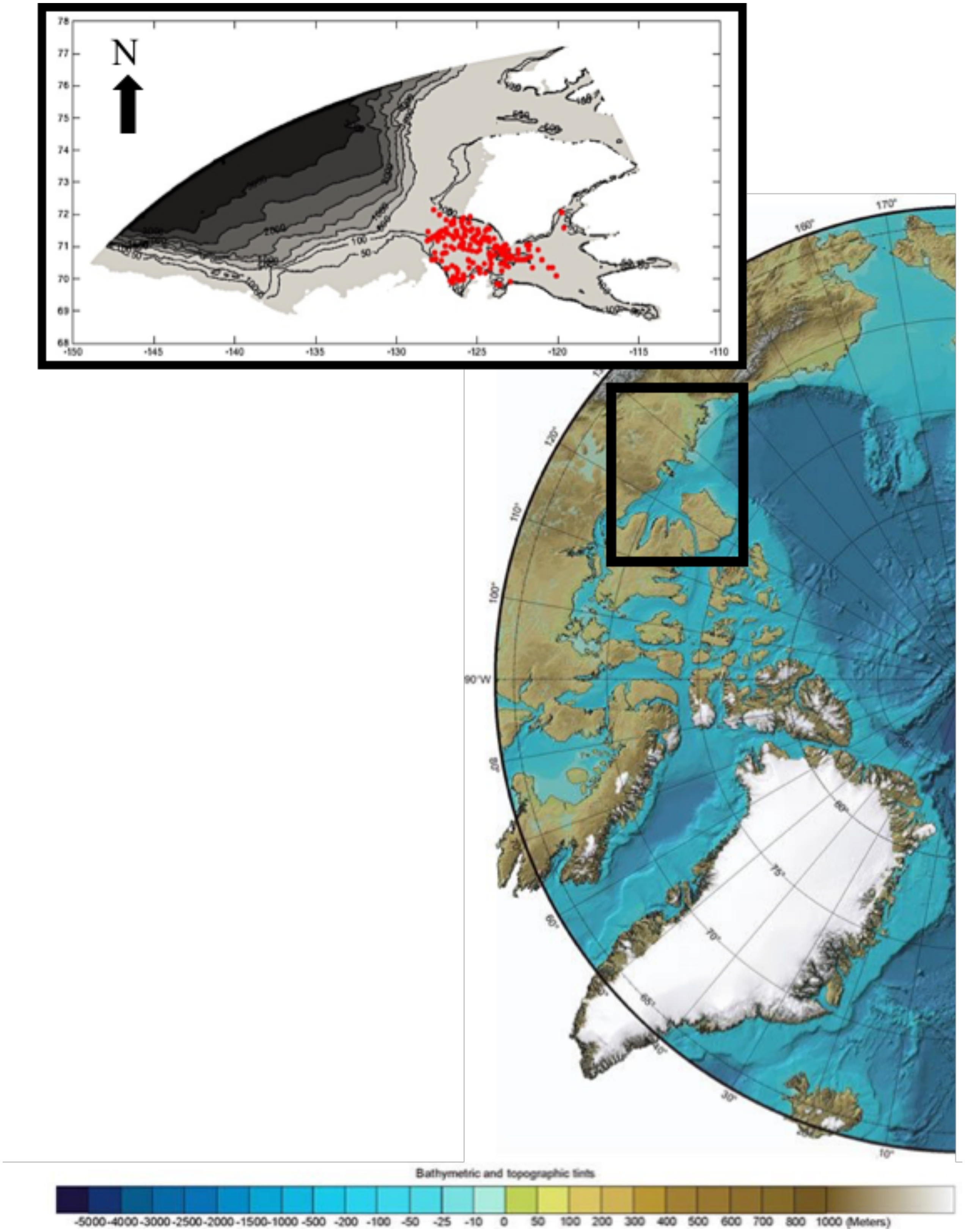

Figure 5 : Study location within the Arctic. The Arctic map is the International Bathymetric Chart of the Arctic Ocean resulting from the Intergovernmental Oceanographic Commission (IOC), the International Arctic Science Committee (IASC), the International Hydrographic Organization (IHO), the US Office of Naval Research (ONR), and the US National Geophysical Data Center (NGDC). The map of the Amundsen golf is from Dufresne et al. (in prep). Each red dot represents a sampling station where environmental values have been measured.

We work using a 1D water column configuration with 35 vertical layers of increasing thickness from the surface to the bottom (575 m), from 5 m to 40 m. The biogeochemical module provides prognostic equations of state for two constitutive nutrients, carbon and nitrogen, and 49 functional species: 25 phytoplankton species spread in 6 phytoplankton functional groups, 10 mixotrophs functional species, 11 species of microzooplankton and 3 species of copepod-like metazoan zooplankton (here after referred as numerical mesozooplankton species #47, #48 and #49, Fig. 3). It also resolved dissolved and particulate organic matter dynamics. Each functional group presented different size classes and parameters.

2.4.6. Calibration

The range of data used to calibrate the respiration rates were extracted from 6 publication (Bamstedt and Tande 1985; Hirche 1987; Ikeda and Skjoldal 1989; Ikeda et al. 2001; Auel, Klages, and Werner 2003; Alcaraz et al. 2010b) providing mass-specific respiration rates of polar copepods. The whole data set (n=59) comprise respiration rate for four of the main Arctic and North Atlantic species (*C. hyperboreus, C. glacialis, C.finmarchicus, Metridia longa*) as well as data for Arctic zooplankton communities (Alcaraz et al. 2010b). Data for nitrogen excretion came from five publications focusing on species known to perform diapause (Bamstedt and Tande 1985; Head et al. 1988; Ikeda and Skjoldal 1989; Ikeda et al. 2001; Alcaraz et al. 2010a; , n=40). Data sets were standardized to 0°C using the following relationship:

$$M_0 = Mt \times \exp(\frac{E \times (0 \times T)}{k \times (0+273)\times (T+273)}) \tag{4}$$

with M_0 the metabolism at 0°C, M_t the metabolism at the temperature T, E the activation energy in eV and k the Boltzmann Constant in eV. The activation energies were either found or estimated from the literature (*C. hyperboreus, Metridia longa* Hirche 1987, *C. finmarchicus* Marshall & Orr 1958, *C. glacialis* Tande and Henderson 1988).

2.4.7. Validation

The validation of the environmental data is performed by comparing their concentration and timing to in situ data provided by Tremblay et al. (unpublished) as well as from the literature. The validation of the allometric metabolism rates is performed by comparing them to the literature data of laboratory and in the field observations. The validation of the diapause dynamic is done by comparing the month of exit and entry of diapause in the model to the ones observed in the field using literature data.

2.4.8. Sensitivity analysis

A sensitivity analysis is performed on the six parameters (excretion, respiration, grazing, grazing half-saturation, linear mortality and density-dependent mortality) that were adapted to the metazoans. By varying one parameter at a time of ±10%, we compared the annual average biomass in mmol C for the copepod-like species that exhibited a stable and recurrent diapause pattern during one post spin-up year of simulation. We also compared, for the same species, the difference in days of the entry and exit of diapause between the original simulation and modified simulations.

2.5. Results

2.5.1. Environmental dynamic

The water column temperature remains around 0°C below 100 m, all year long. In the surface layer, it varies from below -1°C throughout the winter and spring up to 4.8°C in late June, and then decreases back below -1°C by mid-September. This dynamic creates a thermocline around 30 meters from July until mid-August (Fig. 6a). Both nitrate and silicate concentrations varies in the first 50 m of the water column. Both simulated concentrations starts decreasing abruptly in May at the onset of the shot primary production season (Fig. 6b and 6c). Soon after a nutricline forms around 50 m until the end of September. During the following autumn, surface nitrate stock starts to replenish itself again (Fig. 6b), indicating the end of the productive season while the surface silicate stocks only start to replenish themselves in late-December (Fig. 6c). The concentration of nitrate never reach 0 mmol N while the concentration of silicates in the mid-layer (15 mmol SiO_2 at 125-150m) is lower by a factor two compared to what is observed in the field (30-35 mmol SiO_2 at the same depths, Tremblay et al. 2015b).

2.5.2. Parametrization of respiration and nitrogen excretion

The daily mass-specific respiration rates of the three numerical mesozooplankton species implemented in the model were 1.18×10^{-2}, 8.39×10^{-3} and 5.94×10^{-3} mmol C mmol C^{-1} d^{-1}, within the range of respiration rates given by the literature (Fig. 7a). The calibrated values of mass-specific nitrogen excretion of 6.08×10^{-2}, 4.96×10^{-2} and 4.05×10^{-2} mmol N mmol C^{-1} d^{-1} were at the high end of the range reported by experimental studies (Fig. 7b).

2.5.3. Diapause dynamics

The diapause dynamics for each numerical mesozooplankton species was apparent in the ontogenetic migration pattern between the productive surface layer and the deep refuge during the unfavourable winter. Numerical mesozooplankton species #48 alternated periodically on an annual basis between a short productive season in summer, during which its total biomass increased by a factor of 2, and a prolonged diapause at depth (Fig. 8). The loss of biomass during diapause was less pronounced (10 times smaller than the active state). This numerical species actually produced two cohorts entering diapause at two months' interval (Fig. 9a). The large majority of the active summer biomass started diapause in late-August, whereas a smaller portion of its biomass continued to grow until and in late-October, when they joined the deep-dwelling diapausing population (Fig. 9b).

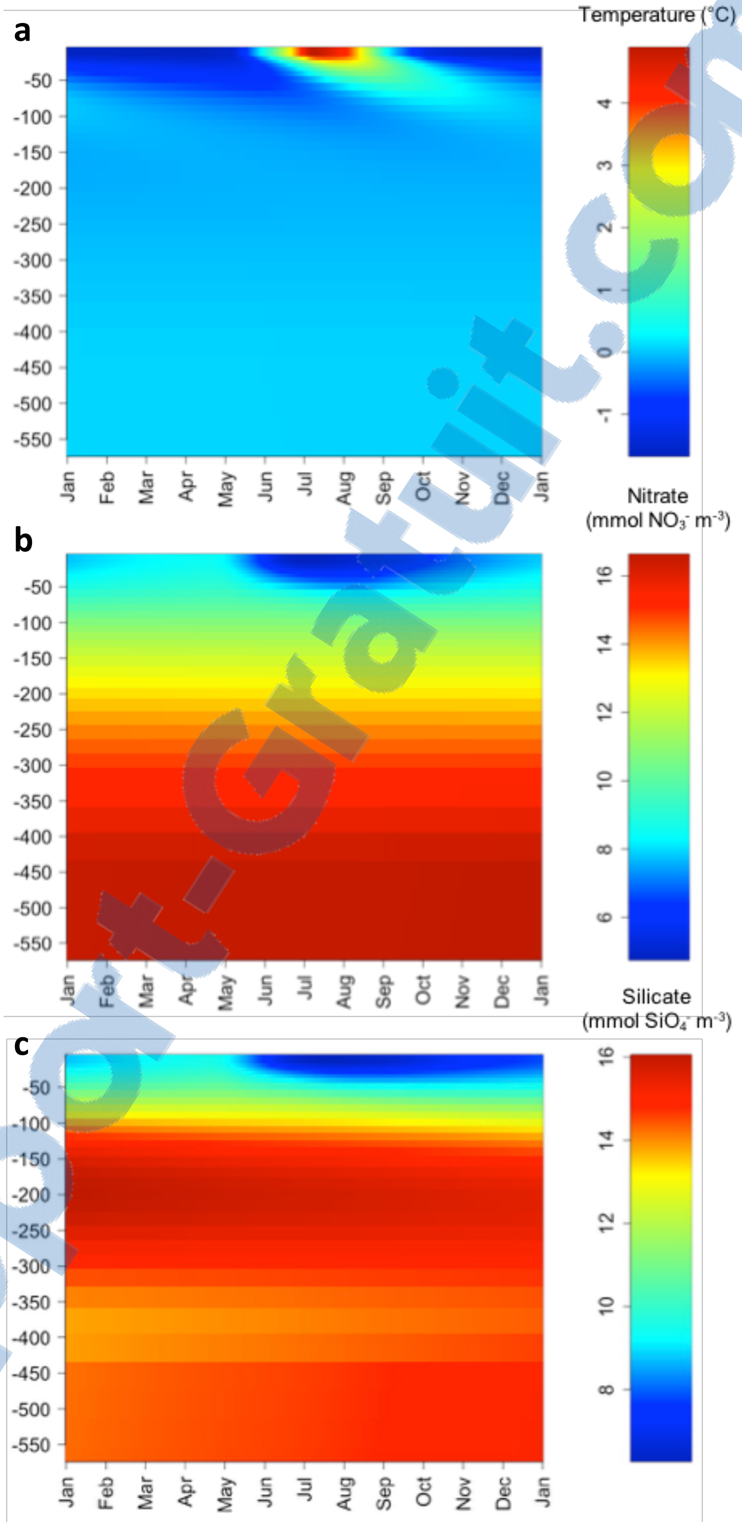

Figure 6 : Post spin-up annual cycle of the model. The temperature a), Nitrate b) and Silicate c) exhibits a seasonal and stratified dynamic.

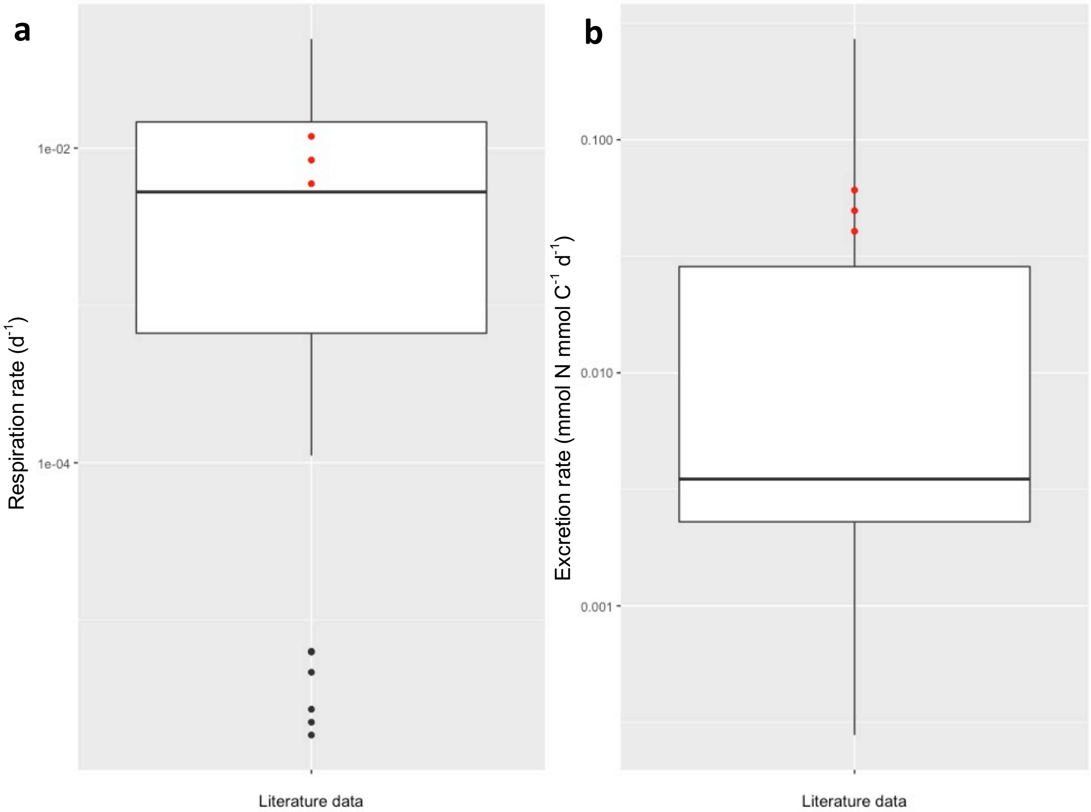

Figure 7 : Comparison of the numerical metazoans metabolisms with the literature data. The red dotes for both the respiration rate a) and excretion rate b) are the rates of the numerical metazoans. The black dots in a) represents measurements found in the literature that are out of the main range of the observed rates.

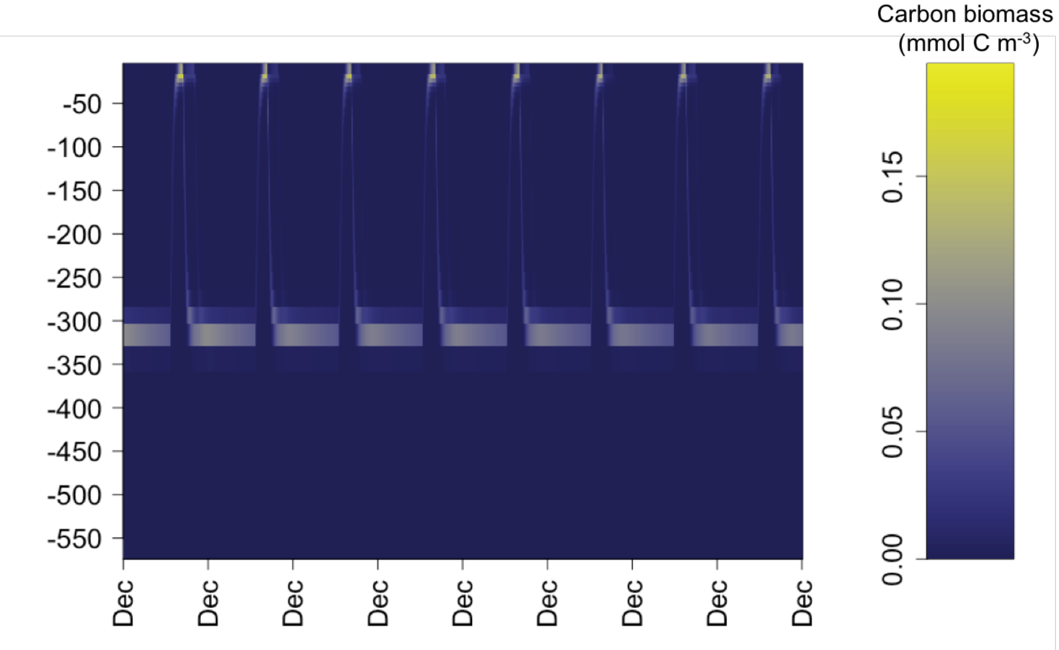

Figure 8 : Migration pattern of the copepod-like numerical species of 1635 µm of diameter that exhibits a recurring realistic diapause pattern.

Since the vertical layer thickness increases with depth in the 1D setup, there is an apparent decrease in concentration because of mass conservation. During an annual cycle of production, the migration schedule matches the timing of the C:N ratio, since the latter is controlling the entrance into and exit from diapause (Fig. 9a). Until the C:N ratio reaches the lower threshold of 6.5, the numerical metazoan species remain in diapause. As soon as this lower threshold is reached, the biomass is transferred into their active compartment and starts migrating towards the target depth of 15 m. This ontogenetic migration is completed within two weeks. In the meantime, there is no feeding since the prey concentration is too low, so there is no nitrogen excretion. Because the respiration of this migrating biomass remains fueled by the carbon pool (lipid reserves), the C:N ratio continues to decrease. Until feeding resumes (8.64×10^{-7} mmol C m^{-3} d^{-1}) and the metazoan species will start accumulating carbon and hence actively excretes nitrogen. This leads to an increase in the C:N ratio by early July for the numerical mesozooplankton species #48, when most of the biomass has reached the productive surface layer. Then, as soon as the C:N ratio exceeds the upper threshold of 12, all the biomass from this model layer is transferred into the diapause compartment. At this moment the biomass starts migrating towards the resting depth of 300 m, excretion stops and respiration continues at a reduced rate (see Methods), which explains the change in the C:N slope (Fig. 9a).

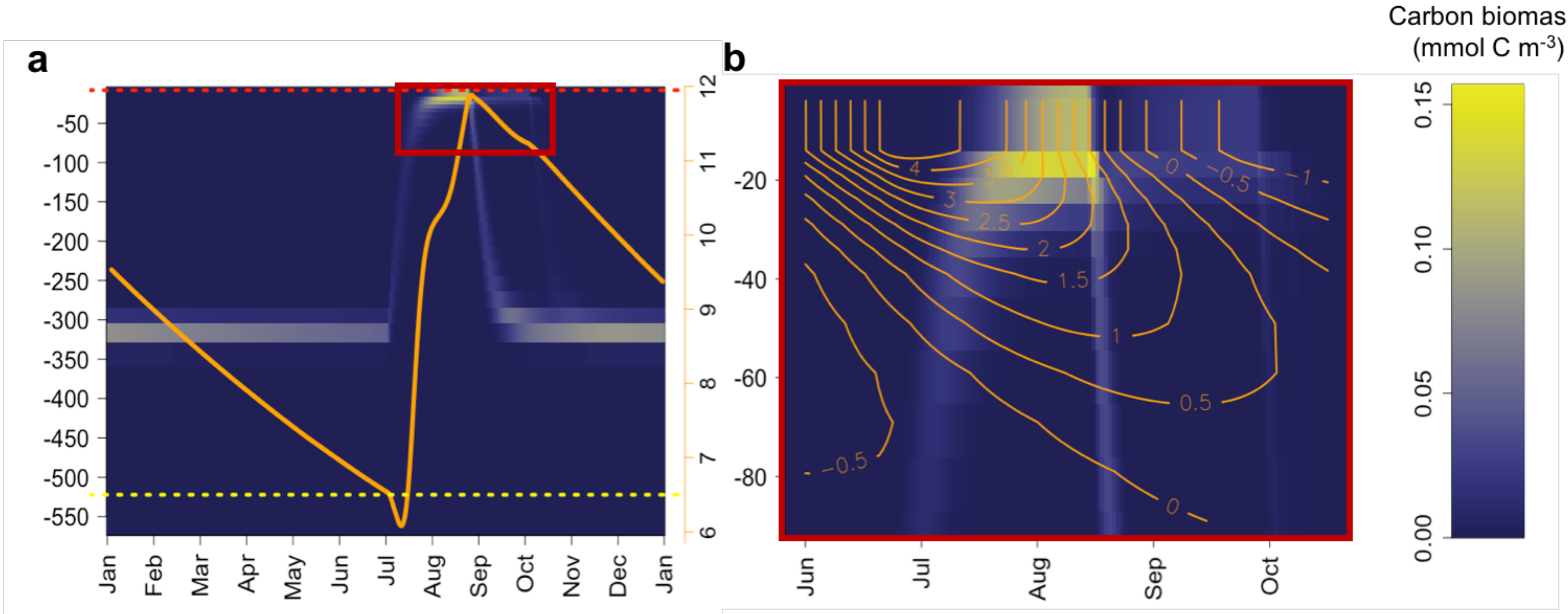

Figure 9 : Migration pattern and C:N dynamic (orange line) over one year for the copepod-like #48 (a) biomass dynamic over the thermocline in summer and early fall (b). The dotted yellow and red lines in a) represents respectively the high and low C:N ratio thresholds. The orange lines in b) represents the isothermes in degree Celsius.

2.5.4. Trophic relationships

The model takes into account complex trophic relationships based on size relationships between preys and predators (see Methods; Fig. 3). Not all numerical species managed to thrive in the 1D water column model forced by in situ data (Fig. 4), but those that do are organized into six cluster characterized by stronger trophic interactions. Clusters reflect the size range of preys and predators, where the top predators are the three numerical mesozooplankton species, labelled 47, 48 and 49.

The addition of a numerical mesozooplankton species that express the functional trait of diapause has a direct impact on the dynamics of the species involved in its trophic chain (Fig. 10). In order to see the pattern of this impact more clearly, we choose to look at three species of the food web, mesozooplankton #48, its microzooplankton prey #40 and phytoplankton #15 preyed upon by that microzooplankton. When the numerical mesozooplankton species does not express diapause, the vertically integrated biomasses of numerical diatom #15 and microzooplankton #40 reveal a simple relationship. The pattern is unimodal, with the microzooplankton biomass following by almost two months the peak in diatom biomass, while the mesozooplankton does not thrive (Fig. 10a). When the numerical mesozooplankton species express diapause, the restriction of feeding on the microzooplankton species in summer produces a cascading effect by releasing some grazing pressure on the diatom species, which allows the latter to produce a noticeable fall bloom (Fig. 10b). Even if the model had a constant remineralisation rate, allowing a possible regenerated production, in our case the trophic cascade resulting from the diapause allows a new production. Since none of the silicate of nitrate concentrations reaches 0, the release of grazing pressure from the microzooplanktons enables some phytoplankton species to create a second new production in fall. Autumn production does not last long though, since environmental conditions became unfavourable by then. The mesozooplankton biomass buildup is saved for the next summer and allows for a sustainable seasonal cycle of production.

2.5.5. Implications for planktonic production

The comparison of the vertically integrated biomass of all the species forming the phytoplankton and microzooplankton functional groups between the simulation without (Fig. 11a), and with (Fig. 11b) a thriving numerical mesozooplankton species able of diapause shows a limited impact of the implementation of this trait on the overall production of the planktonic ecosystem. For the biomass of phytoplankton, there is no significant changes between both scenarios (Wilcoxon test p-value = 0.122). For the microzooplankton, both scenarios produced significantly different biomasses (Wilcoxon test p-value = 1.3×10^{-9}), but the size effect remains limited with a relative reduction of 3.6% for the diapause scenario.

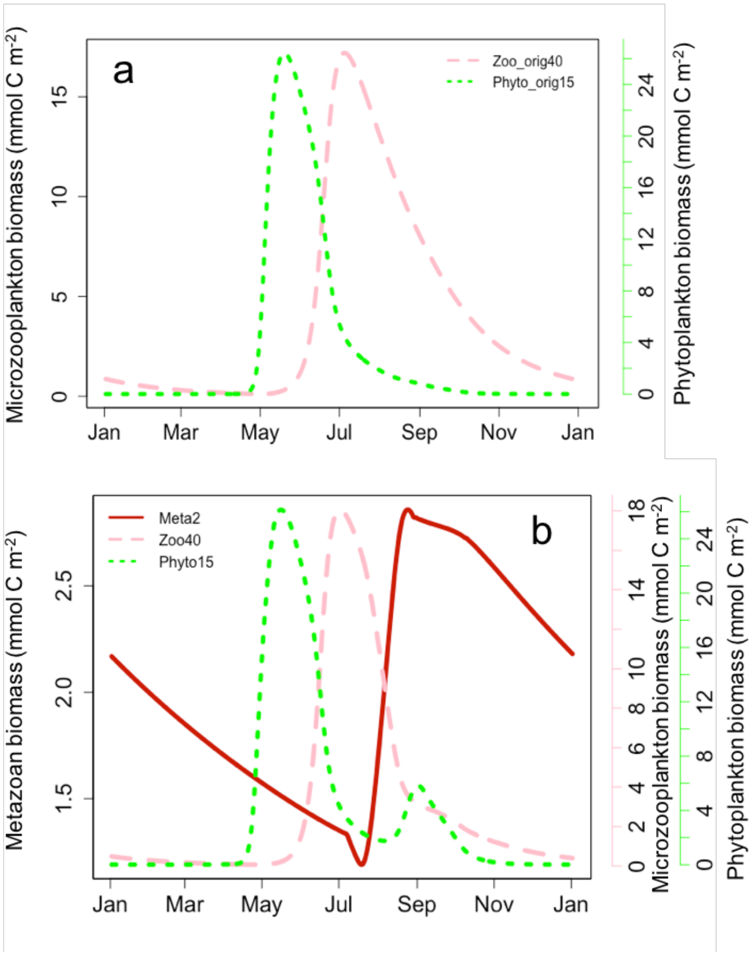

Figure 10 : Impact of the diapause trait on the phenology. (a) Trophic chain dynamic of two species from the scenario without diapause (b) versus trophic chain dynamic of the same two species in a scenario with the implementation of the functional trait of diapause.

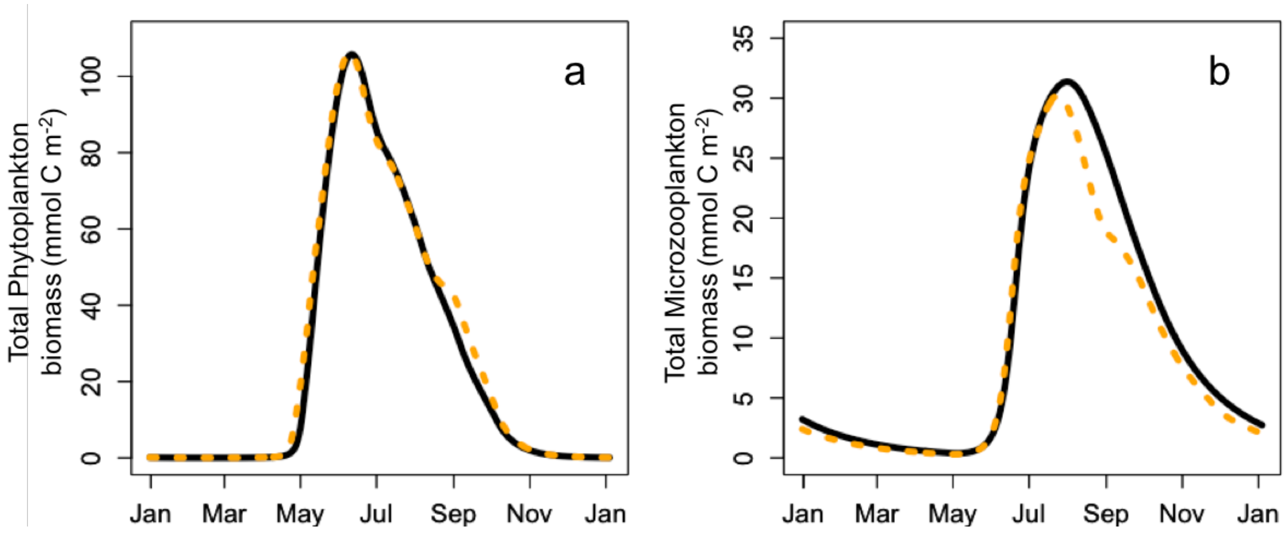

Figure 11 : Impact of the diapause on the biomasses. (a) Differences in total biomass between the original run and the mesozooplankton run for the whole phytoplankton compartment (b) and the whole microzooplankton compartment. The back line represents a simulation without the surviving metazoans while the dashed red line is the simulation with surviving metazoans doing the diapause.

2.5.6. Sensitivity analysis

The biomass of the whole mesozooplankton functional group is sensitive to the scaling factors of the allometric equations of respiration, excretion and grazing rates. It is worth noting that while we estimated sensitivity by computing the relative differences in carbon biomass, the nitrogen excretion had a noticeable impact. Since both respiration and excretion rates are key metabolism processes governing the timing of the diapause in our implementation, it appears that a small change in any of those rates would induce a change in the synchronism between the numerical mesozooplankton species and their prey species. This ultimately influences the yearly biomass production of the numerical mesozooplankton compartment by -24% to +27.4% for a variation of respectively -10% to +10% of the respiration rate (Figure 12).

The diapause timing of the numeric mesozooplankton species #48 that expressed a realistic diapause pattern is mostly sensitive to the respiration and grazing rates scaling factors (Table 2). Variations of the grazing half-saturation coefficient, mortality rate and density-dependent mortality coefficient did not have a strong impact on the diapause timing.

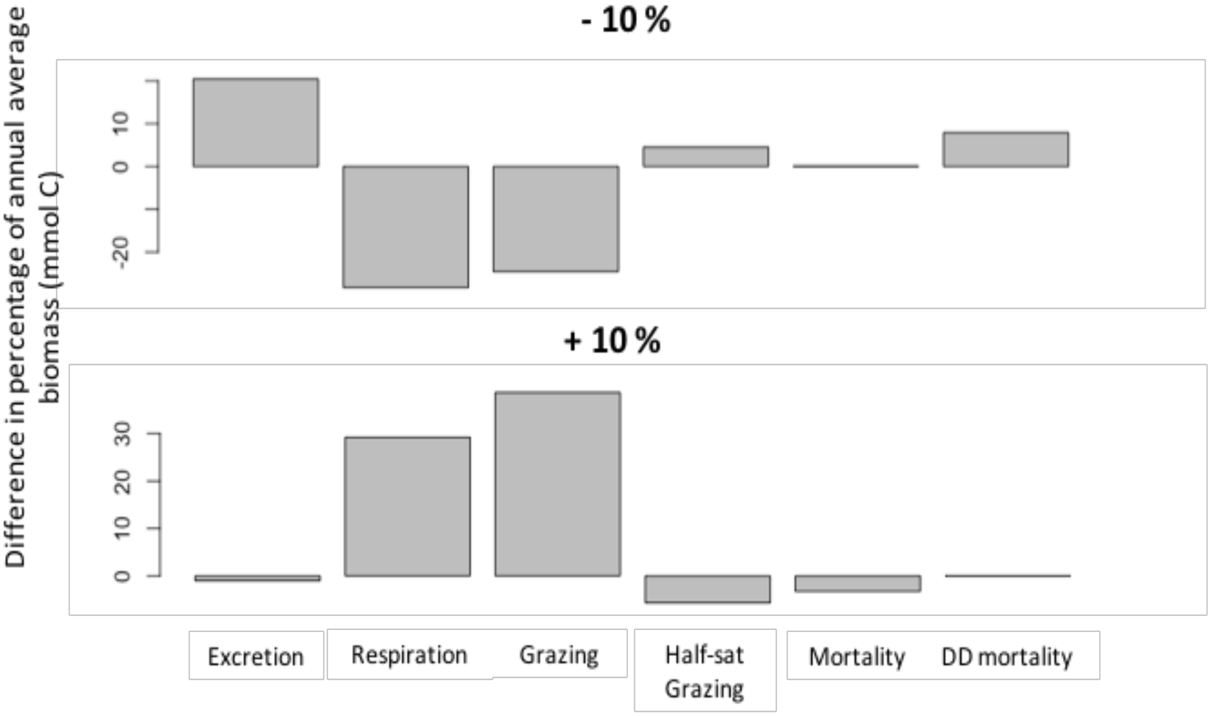

Figure 12 : Sensitivity analysis on the metazoan compartment. In this analysis, we compared the annual average of biomass in mmol C of the metazoan compartment from our regular scenario (realistic diapause) to scenarios with variations of + and – 10% of each of the parameters that we adapted for the allometry of the metazoans. By doing so we compared the impact of the excretion rate, respiration rate and grazing rate, grazing half-saturation, linear mortality and density-dependent mortality separately.

Table 2 : Sensitivity of the timing in days of entry and exit of diapause for the numerical mesozooplankton species (#48). This table shows the difference in days between the entry/exit dates of our regular scenario and a variation of + and -10% of the six parameters adapted to the allometry of metazoans. The star indicates a diapause pattern that was too late in comparison with the once observed into the field.

	Metazoan #48			
	-10%		10%	
	Exit	Entry	Exit	Entry
Excretion	-3	-0	-2	-7
Respiration	+41*	+67*	-35	-22
Grazing	+8	+9	-10	-14
Grazing half-saturation	0	-3	+1	-1
Regular mortality	0	-2	+1	-1
Density-dependent mortality	-1	-5	0	0

2.6. Discussion

In order to reproduce the diapause trait that would allow the survival of the species performing it, we faced two challenges: reproducing (1) a realistic arctic environmental dynamic and (2) a realistic metazoan mesozooplankton metabolism and life-cycle strategy.

Our model represented a numerical environment that was highly seasonal, strongly stratified during summer and typical of an arctic sea. The formation of a thermocline during the summer as well as the temperature amplitude given by the model (Fig. 6a) is in accordance with the field observations (see figure 2b of Darnis and Fortier 2014). The dynamic of the nitrate concentration (Fig. 6b) are also in accordance with what is observed in the Amundsen Gulf (see figure 8a of Tremblay et al. 2015). However, the lowest nitrate concentration never reaches 0 even within the surface layer, which is usually the case in the field. Could be explained by the low concentration of silicates present in the model into the mid-layer depths (100-150m). This low concentration limits the diatoms primary production and hence their nitrogen uptake. Nevertheless, the dynamics of both of these nutrients seems in accordance with what is observed in the Amundsen Gulf (Carmack and Macdonald 2002). Despite those limitations, we were able to represent a simplified arctic environment. Then we were able to test whether the metabolism and diapause strategy of numerical mesozooplankton species were realistic.

2.6.1. Realistic allometric relationships

The use of allometric relationships allows to efficiently represent the various physiological rates and processes for different species spread along a large size range (Guiet, Poggiale, and Maury 2016; Andersen et al. 2016; Blanchard et al. 2017). By using an allometric relationship specific to pelagic mesozooplankton (Moloney and Field 1989), we were able to simulate realistic mass-specific respiration rates for one numerical copepod-like species (Fig. 7a). The value found for our second copepod-like functional species is very close to the values found by Danis and Fortier (2012) into the Amundsen gulf for zooplankton larger than 1000 µm

($8.55x10^{-3}$ mmol C mmol C^{-1} d^{-1}). With these respiration rates, we were able to calibrate the excretion rate first estimated from a meta-analysis of pelagic zooplankton excretion rates (Vanni and McIntyre 2016) that were essential for implementing the diapause dynamics. While standing on the upper limit of the range, these excretion rates are still within observed values for the calanoïd copepods that dominate the Arctic and boreal mesozooplankton communities (Fig. 7b). With correct metabolisms and our assumptions on the diapause, we were able to reproduce a realistic diapause dynamics (Fig. 8).

2.6.2. Realistic diapause phenology

Darnis and Fortier (2012) found that the large fraction of mesozooplankton (>1000µm) was going out of diapause between early May to early July and was going back into diapause as soon as July, with the whole population at depth in October. Duzetter et al. (2017), studied temporal series of copepods caught in sediments traps from the Beaufort Sea continental shelf. They corroborate the migration timing found by Darnis and Fortier (2012). Our second numerical mesozooplanktonic species (#48) exits diapause in late June with a first (the largest) cohort going into diapause in mid-August, while a second cohort went diapausing at depth in mid-October (Fig. 9a). The simulated diapause duration was comparable with the observed patterns in the Amundsen Gulf. The generation of two cohorts is explained by the presence of vertical gradients in temperature and prey concentrations between 15 and 40 m (Fig. 9b). The model is using an Arrhenius-like relationship between metabolic rates and the temperature. With a higher temperature toward the surface, the metabolism rates were higher as well. These gradients meant that the mesozooplankton biomass started to be ready for diapause first at the upper surface layer. By the time it migrated down, some of the biomass from the layer underneath has been diffused by turbulent processes in the upper layer. This biomass had a distinct C:N ratio and continued its growth. This process continued until the vertical structure in environmental conditions has been eroded in autumn, hence allowing the biomass remaining in the surface layers (between 0 and 50 m) to uniformly reach the upper C:N threshold and start its descent at depth. This is coherent with the work of Darnis and Fortier (2012), showing smaller size fraction zooplankton (200-1000 µm in the study) going later into diapause than their larger counter-parts (>1000 µm in the study). This dynamic could represent the different migrating cohorts related to the ontogenic cycle of the copepods (Darnis and Fortier 2014). The respective mechanisms responsible for this are likely different though, and this raises some questions relative to the eventual behavior of the model in a more dynamic 3D implementation when coupled to a regional circulation model.

Nonetheless, by not being at the surface at all times as in most of the NPZD-type biogeochemical models, our diapausing mesozooplanktonic functional group also impacted the phenology of several microzoo- and phytoplanktonic and compartment. From there, we investigated the possible impacts of the functional trait of diapause on a numerical planktonic community composed of various species of primary and secondary producers.

Modulation of the grazing pressure changes the phenology of some of the microzooplankton and large phytoplankton (diatom) species. While grazing on their microzooplanktonic preys, numerical mesozooplankton species exhibiting a realistic diapause pattern enable a secondary fall bloom for some phytoplankton species by releasing them from the grazing pressure of their microzooplankton predator (Fig. 10b). In our model, the numerical mesozooplanktonic species feed essentially on microzooplanktonic species, owing to their size range (e.g. Broglio et al. 2003; Mitra and Flynn 2005). However, it is known that the dominant Arctic *Calanus* congeners are mostly herbivorous (Darnis and Fortier 2014). Our current set of numerical functional traits did not allow the survival of diatom species larger than 22 µm in diameter. This is due to a specific numerical limitation of the use of the nitrogen quota that do not allow the survival of phytoplanktons bigger than 22 µm. Hence our numerical mesozooplankton species could only rely on their microzooplankton prey. The impact of the diapause on the biomass would only results from the release of the grazing pressure of the microzooplankton over their phytoplankton prey. In the meantime, this modulation of grazing pressure had a limited impact on the whole microzooplankton biomass while it did not on the whole phytoplankton biomass. This is again due to the fact that our mesozooplanktonic functional species only feed on a handful of microzooplankton species that in turn feeds on a few phytoplankton species (Fig. 4). This is one of the limitation of our configuration of the model in representing and Arctic ecosystem. Since we only have one metazoan functional species that does exhibit a realistic pattern, with a limited number of preys, its impact on the whole microzooplankton and phytoplankton biomasses is limited. However, changes in the phytoplankton phenology as a group was still noticeable.

Since it has been shown that the Amundsen Gulf is highly nitrogen-limited during the productive season (Tremblay and Gagnon 2009; Tremblay et al. 2012; Tremblay et al. 2015a) it is assumed that the phenology of the plankton is essentially *bottom-up* driven. The change of phenology observed in our research highlights the possible *top-down* control that the zooplankton has over the phenology of some phytoplankton species. This is consistent with previous work done with DARWIN model where, on one hand, the nutrient limitation had a strong *bottom-up* control on the number of size classes of functional phytoplankton species that could coexist, whereas on the other hand, the grazing regulation would modulate the phenology of the thriving species during the productive season (Prowe et al. 2012; Ward et al. 2014).

This offers an alternate hypothesis to the *bottom-up* trigger of the Arctic fall bloom hypothesis. Indeed, the work of Ardyna et al. (2014) related the increase of occurrence of fall bloom into the Arctic with an increase of strong winds events. These strong winds events should break the stratification and bring additional nutrients at the euphotic layer, enabling a second new primary production in fall. In our case, we observe a small increase of the whole biomass of phytoplankton in fall, which is accompanied by a small increase in chlorophyll a (not shown here). This is the result of the indirect *top-down* control of the mesozooplankton enabling a second new primary production in fall. With the possible trend of a smaller arctic plankton community (Leu et al. 2011), this is a plausible scenario where “big diatoms” are not present in fall, which forces the dominant arctic copepods to rely on microzooplankton, which enables the “small” phytoplankton species to thrive until the water column become too mixed and the formation of sea ice.

Ours results indicates the possible relevance of taking into account the *top-down* control of the zooplankton when considering the population dynamics of some species of interest (Olli et al. 2007; Friedland et al. 2016; Steinberg and Landry 2017) and more work need to be done in that regard. Ultimately, the mechanisms regulating the diapause dynamics will modulate the control of the mesozooplanktonic species on the whole system. Here we used only internal processes to infer on the migration timing, but one species have different diapause timing in different regions, implying that there could be environmental cues for the exit of diapause (Johnson et al. 2008; Daase et al. 2013).

In this context, the use of the C:N ratio within the lipid accumulation window framework was a satisfactory approximation to define the potential diapause duration at depth for one numerical mesozooplankton species. However, it revealed to be too sensitive to allometric relationships and minor deviations of the metabolic rates (Table 2, Fig. 12) to efficiently represent several coexisting numerical mesozooplankton species spanning a realistic range of body size. Dezutter (2017) showed that Arctic *Calanus* congeners seem able to exit diapause when the environmental conditions are favorable. To be evolutionary successful, the diapause life-cycle strategy has to allow the individuals to escape into a state of diapause in advance of the establishment of detrimental environmental conditions. This should involve physiological mechanisms controlled by the internal status of the organism and as a result the link to the level of lipid stores in individual copepods remains a plausible mechanism. However, this strategy also involves the ability to exploit favourable environmental conditions as soon as they are prevailing. As a result, reactivity to environmental cues is likely to be an evolutionary advantage for exiting the diapausing state. One possible way to implement such a control in the model would be to take into account the downward flux of particulate organic matter. Either absolute concentration thresholds or variations in the rate of change with time are common control mechanisms in animals. Our work being a proof of concept, it is the first step toward a more realistic representation of an Arctic pelagic ecosystem.

Even though the model itself is not completely representative of an Arctic plankton community yet (missing the ice algae bloom and large diatoms species) the addition of the carbon flux associated to the diapause (defined recently as “the lipid pump”, Jónasdóttir et al. 2015) may be a locally important component of its biogeochemistry (Darnis and Fortier 2012; Visser, Grønning, and Jónasdóttir 2017). Darnis and Fortier (2012) found for the Amundsen gulf that the diapause related carbon flux was of the same order of magnitude than the carbon flux associated with the particulate organic detritus sink. Jonasdottir et al. (2015) and Visser, Grønning, and Jónasdóttir (2017) reached to the same conclusion off the coast of Spitsbergen.

2.7.Conclusion

We demonstrated the feasibility of implementing the functional trait of diapause into a biogeochemical model in a 1D configuration. It confers to a mesozooplankton larger than 1000 µm the ability to survive until the next productive season. The fact that no mesozooplankton larger than 1000 µm survives in our control run (without the diapause) highlights it necessity once a species reaches a certain size. This could help in the understanding of the range of behavior observed in copepods in the Arctic depending on their size (Darnis and Fortier 2014). We showed that with simple assumptions and correct copepod-like metabolism it was possible to have realistic diapause and even the emergence of an ontogenetic migration-like patterns. While the impact of the diapause trait seems limited on the biomass of the planktonic ecosystem as a whole, the inclusion of this trait had a significant impact on the phenology of some planktonic species. Even though it is still limited to a few functional species, the switch from an unimodal to a bimodal phenology showed a potential mechanism by which such models could facilitate a secondary fall bloom that is otherwise damped by the constant grazing pressure of the microzooplankton on the phytoplancton. Moreover, the seasonality and the vertical structuration of the biogeochemical fluxes of the main elements (carbon, nitrogen) would be altered by the changes in the mesozooplankton metabolism and its vertical ontogenetic migrations (Lipid pump; Jónasdóttir et al. 2015). The next step will be to include this implementation into a study looking at the processes involving ammonium and bacteria.

Our results also suggest a possible way to test our model assumptions by measuring *in situ* the relative contribution of the new and regenerated primary production in presence or absence of actively growing mesozooplankton. Indeed, according to our assumptions, the growth of mesozooplanktonic species rapidly accumulating lipids should theoretically lead to an increase in dissolved organic nitrogen and regenerated primary production (lipid “shunt”; Jónasdóttir et al. 2015).

3. Conclusion générale

Bien que les mécanismes de contrôle de la stratégie de diapause des copépodes et leur conséquences écologiques aient déjà suscité plusieurs études (Conover and Huntley 1991; Hirche 1996; Johnson et al. 2008; Maps et al. 2011; Maps, Record, and Pershing 2014; Baumgartner and Tarrant 2017), notre étude est la première à mettre en place le trait fonctionnel de la diapause dans le contexte d'un modèle biogéochimique de type Eulérien. En simulant correctement le métabolisme d'espèces numériques analogues aux copépodes planctoniques ainsi qu'en suivant de simples hypothèses sur la régulation de la diapause, nous avons pu obtenir une espèce fonctionnelle présentant une dynamique de diapause comparable à celles observées dans notre zone d'étude, le Golf d'Amundsen. La comparaison entre des simulations avec et sans le trait fonctionnel de la diapause ont montré que ce trait permet la survie d'une espèce fonctionnelle de métazoaire, modifie la phénologie de certaines espèces fonctionnelles planctoniques et a un impact sur la biomasse totale du compartiment microzooplanctonique (bien que celui-ci reste minime).

Le fait que le trait de la diapause permette à nos espèces de métazoaire de survivre plusieurs années est directement lié à l'accumulation de carbone que nous utilisons comme proxy d'une accumulation de réserves énergétiques lipidiques. En plus de cette accumulation d'énergie, l'autre clef du succès de leur stratégie de diapause est la réduction de leur métabolisme ainsi que de leur mortalité en raison de leur migration en profondeur (réduction de la prédation visuelle). La survie d'une espèce fonctionnelle de mesozooplancton et l'émergence d'un synchronisme entre cette espèce fonctionnelle et ses proies conduit à un changement dans la phénologie totale du compartiment de ses proies.

3.1.Changement de phénologie

Dans les modèles NPZD classiques, la prédation n'est qu'un terme de fermeture pour le plancton et peu d'attention est porté à la dynamique zooplanctonique elle-même. Bien que la dynamique des communautés planctoniques arctiques soient en premier lieu contrôlée par un contrôle ascendant de l'environnement, notre étude montre que des variations dans la pression de prédation d'un espèce clef telle qu'une espèce fonctionnelle de copépode peut moduler la dynamique de l'ensemble du compartiment planctonique du modèle. Avec une modulation de la pression de prédation contrôlée par la sortie et l'entrée de diapause, on observe le passage d'une dynamique unimodale vers une dynamique bimodale pour certaines espèces fonctionnelles impliquées dans une courte chaîne trophique. Ceci est cohérent avec les observations démontrant que la pression de prédation permet de réguler la phénologie sur une échelle saisonnière (Buitenhuis et al. 2006; Olli et al. 2007; Mariani et al. 2013; Friedland et al. 2016; Menden-Deuer and Kiørboe 2016). Néanmoins, l'impact est différent entre les compartiments phytoplanctonique et microzooplanctonique et le changement de phénologie du phytoplancton ne résulte pas d'une action directe du broutage du mesozooplancton. Ceci est dû au fait que les espèces numériques de mesozooplancton qui survivent dans nos simulations devaient se nourrir sur des espèces microzooplanctoniques car le modèle ne permet pas (encore) la survie de espèces phytoplanctoniques de tailles suffisantes pour être ciblées par la fonction d'ingestion (telles que les diatomés pénnées et centrique) qui sont normalement les proies principales des espèces de *Calanus* arctique (Campbell et al. 2009; Darnis and Fortier 2014). Ainsi, les changements dans la phénologie phytoplanctonique sont dû à un relâchement de la pression de prédation de leurs prédateurs microzooplanctoniques, eux même consommés par une espèce fonctionnelle de mesozooplancton. Par conséquent, l'impact du trait fonctionnel de la diapause sur la biomasse totale de chaque compartiment planctonique est lui aussi limité.

3.2. Impact sur la biomasse totale planctonique

Sachant que nos espèces fonctionnelles de mesozooplancton se nourrissent essentiellement de microzooplancton, il n'est pas surprenant que l'impact de la diapause sur la biomasse totale de phytoplancton ne soit pas significatif. Cet impact est d'autant plus limité du fait qu'une seule des trois espèces fonctionnelles de copépode présentait un synchronisme avec ses proies. Ceci souligne une autre contrainte inhérente au modèle qui est l'utilisation de relations allométriques afin de reproduire le métabolisme de nos espèces fonctionnelles. Plusieurs études ont montré l'intérêt d'une telle approche en ce qui concerne la modélisation de communautés fonctionnelles diverses (Ward et al. 2012; Barton et al. 2013; Dutkiewicz et al. 2015). Néanmoins, dans notre cas, l'utilisation des même relations allométriques pour différentes classes de taille de métazoaires ne permet d'avoir qu'une seule espèce fonctionnelle présentant une dynamique de diapause réaliste et synchrone avec la phénologie de production de ses proies. Dans notre étude, la diapause est régulée par le compromis (*trade-off*) entre les taux de respiration et d'excrétion. C'est pour cela que dans nos simulations nous n'avons qu'une seule espèce de mesozooplancton dont les relations métaboliques produisent la bonne période de diapause (durée et synchronisme). Les deux autres démontrent un métabolisme trop fort ou trop faible, créant ainsi des dynamiques de diapause chaotiques non réalistes. Ceci corrobore les observations in situ dans lesquelles chaque espèce présente des variations spécifiques de la dynamique de diapause (Darnis and Fortier 2012; Darnis and Fortier 2014) . Des améliorations à notre approche numérique sont requises.

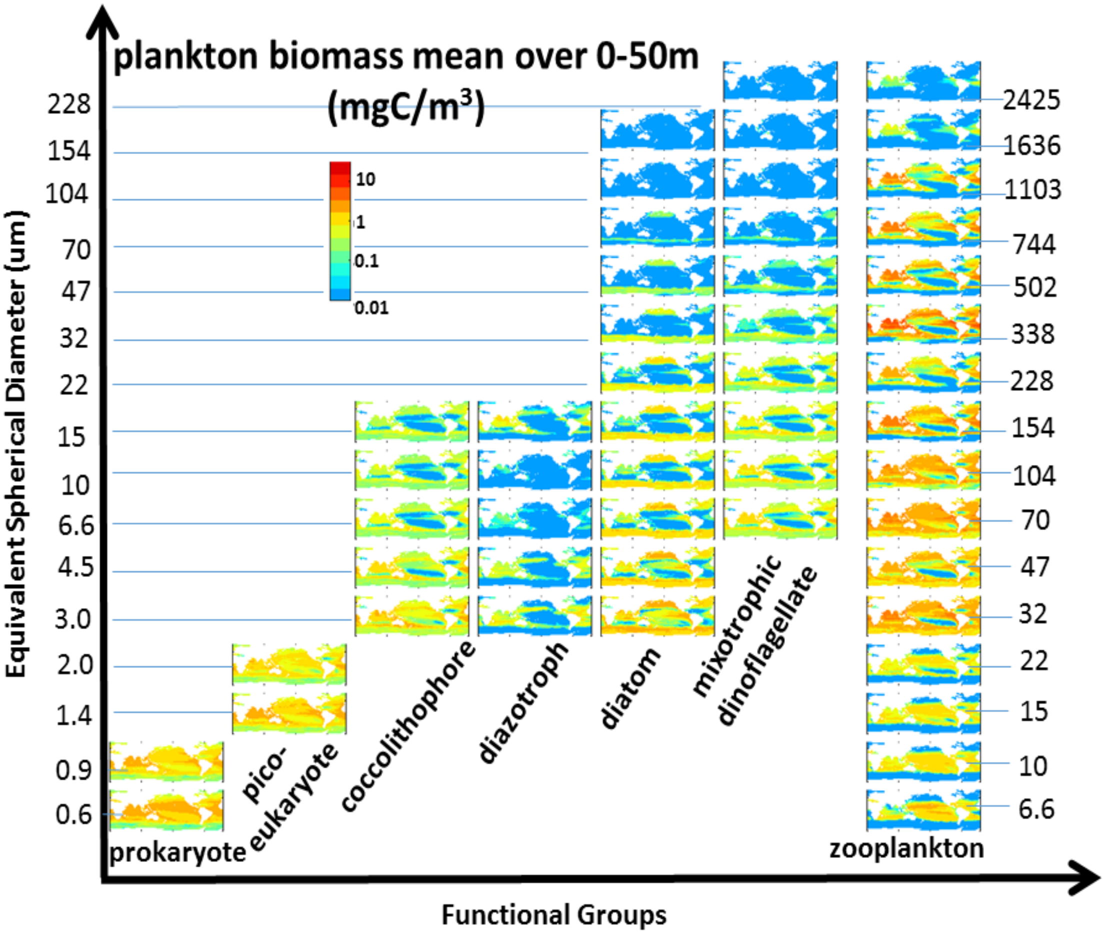

Figure 13 : Distribution mondiale et biomasse d'espèces fonctionnelles d'une configuration de Darwin sans le trait fonctionnel de la diapause. Cette figure provient de données non publiées de Dutkiewizc et al. (unpublished)

3.3. Futures implications

Nous avons pu montrer qu'en suivant l'hypothèse de la fenêtre d'accumulation de lipides et des processus de contrôle internes nous pouvions simuler une dynamique de diapause comparable à ce qui est observé dans le golf d'Amundsen. Néanmoins nous n'avons obtenus un tel résultat que pour une seule espèce numérique alors qu'au moins trois espèces de copépodes sont connus comme faisant de la diapause en Arctique. Ceci nous montre une des limitations de l'utilisation de la fenêtre d'accumulation de lipides. En fait, la fenêtre temporelle définie par les activités métaboliques d'accumulation et de mobilisation des réserves représente la période maximale potentielle durant laquelle notre espèce peut être en diapause. Toutefois, cette espèce pourrait bénéficier d'une sortie hâtive de diapause si les conditions environnementales étaient favorables à son développement. L'analyse des pièges à sédiments mouillés pendant plusieurs années consécutives dans le Golfe d'Amundsen a montré que lors d'années exceptionnelles l'espèce de copépode Arctique dominante *Calanus hyperboreus* peut sortir de sa diapause pour se nourrir sur une production primaire inhabituellement précoce (Fig. 14, Dezutter et al. 2017). Ainsi en utilisant un indicateur externe tel que les variations temporelles de concentration de carbone organique particulaire à la profondeur de diapause, on pourrait permettre aux espèces fonctionnelles de mesozooplancton d'améliorer leur synchronisme avec leurs proies.

Notre étude est un premier pas vers la prise en compte de la diapause dans des modèles biogéochimiques de type évolutif, basés sur la sélection de traits. Dans notre cas, ce trait vient répondre à une des lacunes du modèle DARWIN. Celui-ci n'est pas en mesure de bien reproduire la distribution de tailles du zooplancton à l'échelle mondiale (Fig. 13). Il présente les abondances maximales d'espèces zooplanctoniques de tailles analogues à nos espèces fonctionnelles de métazoaire au niveau des mers équatoriales, alors que dans la réalité ces espèces se trouvent généralement aux niveaux des pôles. Dans ces simulations à grande échelle, les scénarios numériques ne prenaient pas en compte les adaptations métaboliques permettant à des métazoaires d'une taille supérieur à 1000 µm de survivre. Ainsi l'ajout de notre trait fonctionnel dans de telles simulations devrait permettre d'améliorer la prédiction de la biogéographie d'espèces fonctionnelles et de classes de tailles représentatives du mesozooplancton à travers l'océan mondial.

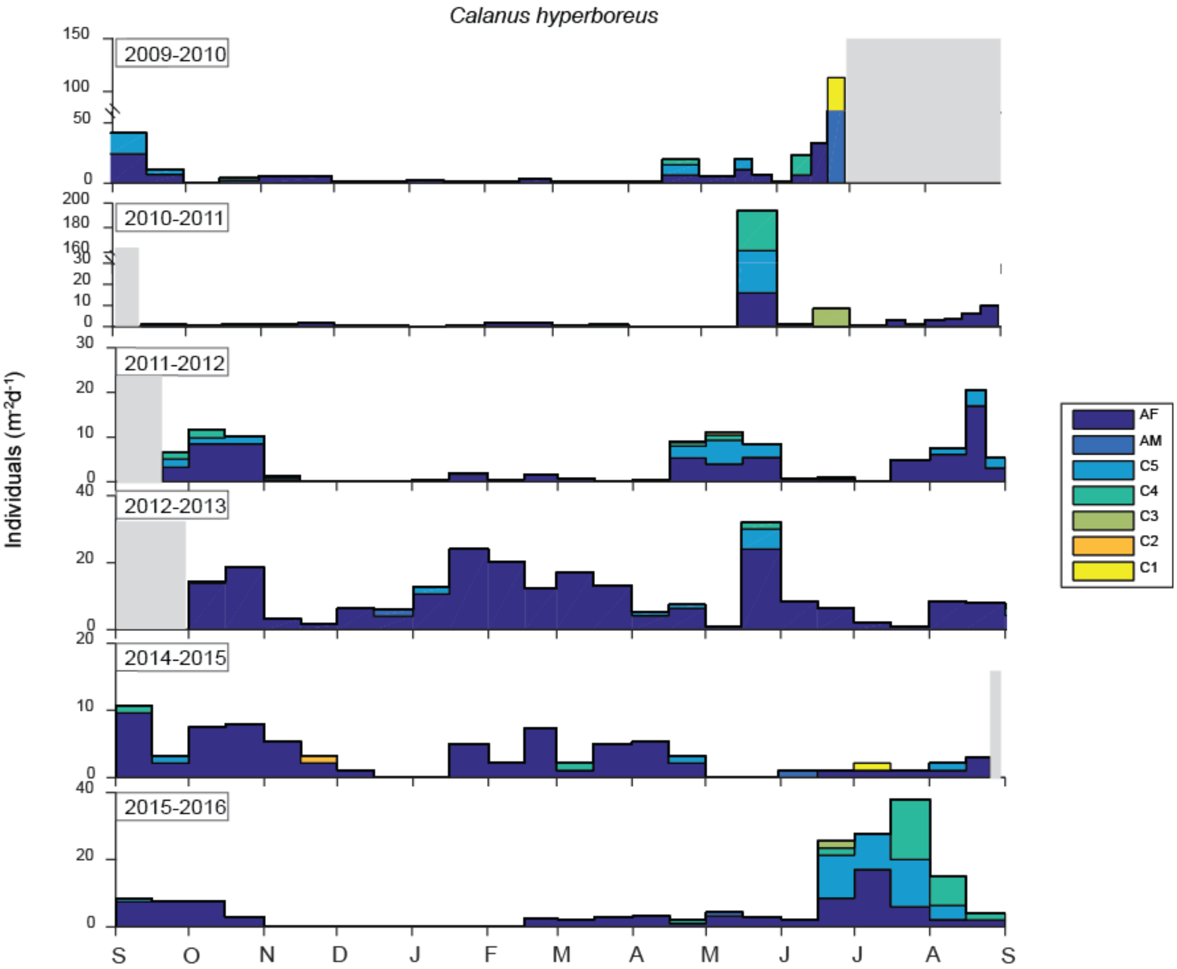

Figure 14 : Proportion de différents stades ontogéniques de *Calanus hyperboreus* présent dans des pièges à sédiments au large de la mer de Beaufort. AF, AM, C1-C5 correspondent respectivement à Femelle Adulte, Mâle Adulte et Copepodite 1 à 5. Cette figure provient des travaux de maîtrise de Dezutter (2017).

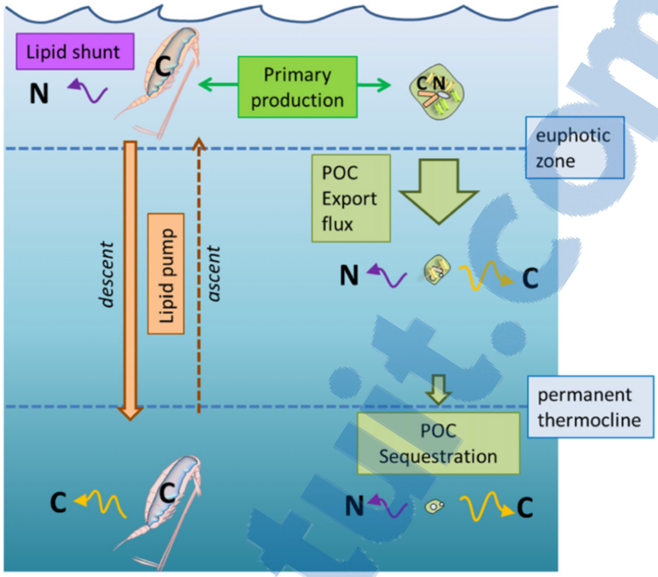

Figure 15 : Pompe à lipide et « court-circuit lipidique » (*lipid shunt*). Tiré de Jónasdóttir et al. (2015).

De plus, avec l'ajout d'un comportement de migration saisonnière, on permet de prendre en compte un flux jusque-là non représenté dans les modèles biogéochimiques : le flux de carbone lié aux espèces zooplanctoniques faisant la diapause, défini par Jonasdottir et al. (2015) comme la pompe à lipides (figure 15). En accumulant de grandes réserves de carbone à la surface pendant la saison productive, une fois que ces espèces migrent en profondeur pour passer en diapause, elles vont respirer ce carbone à des profondeurs où le carbone sera séquestré. Une fois que le modèle sera mieux adapter au contexte arctique (présence de diatomées supérieurs à 22µm, d'algues de glace, implémentation du trait de la diapause dans un context dynamique 3D,) il sera possible d'étudier un flux qui dans la nature est équivalent au flux de carbone lié aux détritus particulaires (Golf d'Amundsen Darnis & Fortier 2012, au large de Svalbard Jónasdóttir et al. 2015). De plus, un autre caractère que nous avons ajouté avec le trait de la diapause est l'excrétion accrue d'azote lors de la synthèse et l'accumulation de lipides en surface. Ce différentiel entre export de carbone vers les profondeur et excrétion à la surface d'azote a été défini par Jonasdottir et al. (2015) comme le « court-circuit lipidique » (*lipid shunt*). Une fois que le modèle présentera des communautés planctoniques plus représentatives de l'Arctique, notre implémentation permettra de tester l'hypothèse selon laquelle la remise en suspension d'azote dissous à la surface stimulerait une production primaire recyclée dans le système.

4. Bibliographie

Alcaraz, M., R. Almeda, A. Calbet, E. Saiz, C. M. Duarte, S. Lasternas, S. Agustí, R. Santiago, J. Movilla, and A. Alonso. 2010a. "The Role of Arctic Zooplankton in Biogeochemical Cycles: Respiration and Excretion of Ammonia and Phosphate during Summer." *Polar Biology* 33 (12): 1719–31. doi:10.1007/s00300-010-0789-9.

———. 2010b. "The Role of Arctic Zooplankton in Biogeochemical Cycles: Respiration and Excretion of Ammonia and Phosphate during Summer." *Polar Biology* 33 (12): 1719–31. doi:10.1007/s00300-010-0789-9.

Andersen, K H, T Berge, R J Gonçalves, M Hartvig, J Heuschele, S Hylander, N S Jacobsen, et al. 2016. "Characteristic Sizes of Life in the Oceans, from Bacteria to Whales." *Annual Review of Marine Science* 8 (1): 150710224004001. doi:10.1146/annurev-marine-122414-034144.

Anderson, T R. 1992. "Modelling the Influence of Food C:N Ratio, and Respiration on Growth and Nitrogen Excretion in Marine Zooplankton and Bacteria." *Journal of Plankton Research* 14 (12): 1645–71. doi:10.1093/plankt/14.12.1645.

Anderson, Thomas R., and Wendy C. Gentleman. 2012. "The Legacy of Gordon Arthur Riley (1911–1985) and the Development of Mathematical Models in Biological Oceanography." *Journal of Marine Research* 70 (1): 1–30. doi:10.1357/002224012800502390.

Ardyna, Mathieu, Marcel Babin, Michel Gosselin, Emmanuel Devred, Luc Rainville, and Jean-éric Tremblay. 2014. "Fall Phytoplankton Blooms," 6207–12. doi:10.1002/2014GL061047.Received.

Ardyna, Mathieu, Michel Gosselin, Christine Michel, Michel Poulin, and Jean-Éric Tremblay. 2011. "Environmental Forcing of Phytoplankton Community Structure and Function in the Canadian High Arctic: Contrasting Oligotrophic and Eutrophic Regions." *Marine Ecology Progress Series* 442 (March 2016): 37–57. doi:10.3354/meps09378.

Arrigo, Kevin R., Donald K. Perovich, Robert S. Pickart, Zachary W. Brown, Gert L Van Dijken, Kate E. Lowry, Matthew M. Mills, et al. 2012. "Massive Phytoplankton Blooms Under Arctic Sea Ice." *Science* 336 (6087): 2012. doi:10.1126/science.1215065.

Auel, H., M. Klages, and I. Werner. 2003. "Respiration and Lipid Content of the Arctic Copepod Calanus Hyperboreus Overwintering 1 M above the Seafloor at 2,300 M Water Depth in the Fram Strait." *Marine Biology* 143 (2): 275–82. doi:10.1007/s00227-003-1061-4.

Balzano, Sergio, Dominique Marie, Priscillia Gourvil, and Daniel Vaulot. 2012. "Composition of the Summer Photosynthetic Pico and Nanoplankton Communities in the Beaufort Sea Assessed by T-RFLP and Sequences of the 18S rRNA Gene from Flow Cytometry Sorted Samples." *The ISME Journal* 6 (8). Nature Publishing Group: 1480–98. doi:10.1038/ismej.2011.213.

Bamstedt, U., and K. S. Tande. 1985. "Respiration and Excretion Rates of Calanus Glacialis in Arctic Waters of the Barents Sea." *Marine Biology* 87 (3): 259–66. doi:10.1007/BF00397803.

Banse, Karl. 2011. "Reflections About Chance in My Career, and on the Top-Down Regulated World." *Annual Review of Marine Science* 5 (1): 120717164858000. doi:10.1146/annurev-marine-121211-172359.

Barton, Andrew D., Andrew J. Pershing, Elena Litchman, Nicholas R. Record, Kyle F. Edwards, Zoe V. Finkel, Thomas Kiørboe, and Ben a. Ward. 2013. “The Biogeography of Marine Plankton Traits.” *Ecology Letters* 16 (4): 522–34. doi:10.1111/ele.12063.

Bashkin, V.N., and O.A. Demidova. 2008. “Biogeochemical Approaches to Environmental Risk Assessment.” In *Encyclopedia of Ecology*, 378–86. Elsevier. doi:10.1016/B978-008045405-4.00768-0.

Baumgartner, Mark F., and Ann M. Tarrant. 2017. “The Physiology and Ecology of Diapause in Marine Copepods.” *Annual Review of Marine Science* 9 (1): annurev-marine-010816-060505. doi:10.1146/annurev-marine-010816-060505.

Bennett, Joseph R, Justine D Shaw, Aleks Terauds, John P Smol, Rien Aerts, Dana M Bergstrom, Jules M Blais, et al. 2015. “Polar Lessons Learned: Long-Term Management Based on Shared Threats in Arctic and Antarctic Environments.” *Frontiers in Ecology and the Environment* 13 (6): 316–24. doi:10.1890/140315.

Blanchard, Julia L, Ryan F Heneghan, Jason D Everett, Rowan Trebilco, and Anthony J Richardson. 2017. “From Bacteria to Whales : Using Functional Size Spectra to Model Marine Ecosystems.” *Trends in Ecology & Evolution* 32 (3). Elsevier Ltd: 174–86. doi:10.1016/j.tree.2016.12.003.

Boetius, Antje, Sebastian Albrecht, Karel Bakker, Christina Bienhold, Janine Felden, M. Fernandez-Mendez, Stefan Hendricks, et al. 2013. “Export of Algal Biomass from the Melting Arctic Sea Ice.” *Science* 339 (6126): 1430–32. doi:10.1126/science.1231346.

Booth, B. C., P. Larouche, S. Bélanger, B. Klein, D. Amiel, and Z. P. Mei. 2002. “Dynamics of Chaetoceros Socialis Blooms in the North Water.” *Deep-Sea Research Part II: Topical Studies in Oceanography* 49 (22–23): 5003–25. doi:10.1016/S0967-0645(02)00175-3.

Broglio, Elisabetta, Sigrún H. Jónasdóttir, Albert Calbet, Hans H. Jakobsen, and Enric Saiz. 2003. “Effect of Heterotrophic versus Autotrophic Food on Feeding and Reproduction of the Calanoid Copepod Acartia Tonsa: Relationship with Prey Fatty Acid Composition.” *Aquatic Microbial Ecology* 31 (3): 267–78. doi:10.3354/ame031267.

Brugel, Sonia, Christian Nozais, Michel Poulin, J. É Tremblay, Lisa A. Miller, Kyle G. Simpson, Yves Gratton, and Serge Demers. 2009. “Phytoplankton Biomass and Production in the Southeastern Beaufort Sea in Autumn 2002 and 2003.” *Marine Ecology Progress Series* 377 (Comiso 2003): 63–77. doi:10.3354/meps07808.

Buitenhuis, Erik, Corinne Le Quéré, Olivier Aumont, Grégory Beaugrand, Adrian Bunker, Andrew Hirst, Tsutomu Ikeda, Todd O’Brien, Sergey Piontkovski, and Dietmar Straile. 2006. “Biogeochemical Fluxes through Mesozooplankton.” *Global Biogeochemical Cycles* 20 (2): 1–18. doi:10.1029/2005GB002511.

Campbell, Robert G., Evelyn B. Sherr, Carin J. Ashjian, Stéphane Plourde, Barry F. Sherr, Victoria Hill, and Dean A. Stockwell. 2009. “Mesozooplankton Prey Preference and Grazing Impact in the Western Arctic Ocean.” *Deep-Sea Research Part II: Topical Studies in Oceanography* 56 (17): 1274–89. doi:10.1016/j.dsr2.2008.10.027.

Carmack, Eddy C., and Robie W. Macdonald. 2002. “Oceanography of the Canadian Shelf of the Beaufort Sea: A Setting for Marine Life.” *Arctic* 55 (SUPPL. 1): 29–45. doi:10.1126/science.100.2596.291.

Comiso, Josefino C. 2012. “Large Decadal Decline of the Arctic Multiyear Ice Cover.” *Journal of Climate* 25 (4): 1176–93. doi:10.1175/JCLI-D-11-00113.1.

Conover, R. J., and M. Huntley. 1991. “Copepods in Ice-Covered Seas-Distribution, Adaptations to Seasonally Limited Food, Metabolism, Growth Patterns and Life Cycle

Strategies in Polar Seas.” *Journal of Marine Systems* 2 (1–2): 1–41. doi:10.1016/0924-7963(91)90011-I.

Daase, Malin, Stig Falk-Petersen, Øystein Varpe, Gerald Darnis, Janne E. Søreide, Anette Wold, Eva Leu, Jørgen Berge, Benoit Philippe, and Louis Fortier. 2013. “Timing of Reproductive Events in the Marine Copepod *Calanus Glacialis* : A Pan-Arctic Perspective.” *Canadian Journal of Fisheries and Aquatic Sciences* 70 (6): 871–84. doi:10.1139/cjfas-2012-0401.

Dahms, Hans U. 1995. “Dormancy in the Copepoda - an Overview.” *Hydrobiologia* 306 (3): 199–211. doi:10.1007/BF00017691.

Darnis, Gérald, and Louis Fortier. 2012. “Zooplankton Respiration and the Export of Carbon at Depth in the Amundsen Gulf (Arctic Ocean).” *Journal of Geophysical Research* 117 (April). doi:10.1029/2011JC007374.

———. 2014. “Temperature, Food and the Seasonal Vertical Migration of Key Arctic Copepods in the Thermally Stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean) GE.” *Journal of Plankton Research* 36 (4): 1092–1108. doi:10.1093/plankt/fbu035.

Darnis, Gérald, Dominique Robert, Corinne Pomerleau, Heike Link, Philippe Archambault, R. John Nelson, Maxime Geoffroy, et al. 2012. “Current State and Trends in Canadian Arctic Marine Ecosystems: II. Heterotrophic Food Web, Pelagic-Benthic Coupling, and Biodiversity.” *Climatic Change* 115 (1): 179–205. doi:10.1007/s10584-012-0483-8.

Droop, M R. 1968. “Vitamin B_{12} and Marine Ecology. IV. The Kinetics of Uptake, Growth and Inhibtition in *Monochrysis Lutheri*.” *J. Mar. Biol. Ass. U.K* 48: 689–733. doi:10.1017/S0025315400019238.

Dufour, Karolane, Frédéric Maps, Stéphane Plourde, Pierre Joly, and Frédéric Cyr. 2016. “Impacts of Intraguild Predation on Arctic Copepod Communities.” *Frontiers in Marine Science* 3 (September): 1–13. doi:10.3389/fmars.2016.00185.

Dupont, F., S. Higginson, R. Bourdallé-Badie, Y. Lu, F. Roy, G. C. Smith, J. F. Lemieux, G. Garric, and F. Davidson. 2015. “A High-Resolution Ocean and Sea-Ice Modelling System for the Arctic and North Atlantic Oceans.” *Geoscientific Model Development* 8 (5): 1577–94. doi:10.5194/gmd-8-1577-2015.

Dutkiewicz, S., A. E. Hickman, O. Jahn, W. W. Gregg, C. B. Mouw, and M. J. Follows. 2015. “Capturing Optically Important Constituents and Properties in a Marine Biogeochemical and Ecosystem Model.” *Biogeosciences* 12 (14): 4447–81. doi:10.5194/bg-12-4447-2015.

Dutkiewicz, Stephanie, J. Jeffrey Morris, Michael J. Follows, Jeffery Scott, Orly Levitan, Sonya T. Dyhrman, and Ilana Berman-Frank. 2015. “Impact of Ocean Acidification on the Structure of Future Phytoplankton Communities.” *Nature Climate Change*, no. July. doi:10.1038/nclimate2722.

Falk-Petersen, Stig, Patrick Mayzaud, Gerhard Kattner, and John R. Sargent. 2009. “Lipids and Life Strategy of Arctic Calanus.” *Marine Biology Research* 5 (1): 18–39. doi:10.1080/17451000802512267.

Flynn, Kevin J., and Aditee Mitra. 2016. “Why Plankton Modelers Should Reconsider Using Rectangular Hyperbolic (Michaelis-Menten, Monod) Descriptions of Predator-Prey Interactions.” *Frontiers in Marine Science* 3 (September). doi:10.3389/fmars.2016.00165.

Follows, Michael J, Stephanie Dutkiewicz, Scott Grant, and Sallie W Chisholm. 2007. “Emergent Biogeography of Microbial Communities in a Model Ocean.” *Science (New York, N.Y.)* 315 (5820): 1843–46. doi:10.1126/science.1138544.

Forest, Alexandre, Virginie Galindo, Gérald Darnis, Simon Pineault, Catherine Lalande, Jean-Éric Tremblay, and Louis Fortier. 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 (1): 161–78. doi:10.1093/plankt/fbq103.

Forest, Alexandre, Jean ??ric Tremblay, Yves Gratton, Johannie Martin, Jonathan Gagnon, G??rald Darnis, Makoto Sampei, et al. 2011. "Biogenic Carbon Flows through the Planktonic Food Web of the Amundsen Gulf (Arctic Ocean): A Synthesis of Field Measurements and Inverse Modeling Analyses." *Progress in Oceanography* 91 (4). Elsevier Ltd: 410–36. doi:10.1016/j.pocean.2011.05.002.

Friedland, Kevin D., Nicholas R. Record, Rebecca G. Asch, Trond Kristiansen, Vincent S. Saba, Kenneth F. Drinkwater, Stephanie Henson, et al. 2016. "Seasonal Phytoplankton Blooms in the North Atlantic Linked to the Overwintering Strategies of Copepods." *Elementa: Science of the Anthropocene* 4: 99. doi:10.12952/journal.elementa.000099.

Gosselin, Michel, Maurice Levasseur, Patricia A. Wheeler, Rita A. Horner, and Beatrice C. Booth. 1997. "New Measurements of Phytoplankton and Ice Algal Production in the Arctic Ocean." *Deep-Sea Research Part II: Topical Studies in Oceanography* 44 (8): 1623–44. doi:10.1016/S0967-0645(97)00054-4.

Gradinger, R., and S. B. Schnack-Schiel. 1998. "Potential Effect of Ice Formation on Antarctic Pelagic Copepods: Salinity Induced Mortality of Calanus Propinquus and Metridia Gerlachei in Comparison to Sympagic Acoel Turbellarians." *Polar Biology* 20 (2): 139–42. doi:10.1007/s003000050288.

Guiet, Jérôme, Jean-Christophe Poggiale, and Olivier Maury. 2016. "Modelling the Community Size-Spectrum: Recent Developments and New Directions." *Ecological Modelling* 337. Elsevier B.V.: 4–14. doi:10.1016/j.ecolmodel.2016.05.015.

Hansen, Agnethe N., and André W. Visser. 2016. "Carbon Export by Vertically Migrating Zooplankton: An Optimal Behavior Model." *Limnology and Oceanography* 61 (2): 701–10. doi:10.1002/lno.10249.

Head, E. J H, A. Bedo, and L. R. Harris. 1988. "Grazing, Defecation and Excretion Rates of Copepods from Inter-Island Channels of the Canadian Arctic Archipelago." *Marine Biology* 99 (3): 333–40. doi:10.1007/BF02112125.

Heath, M R, J O Backhaus, K Richardson, E McKenzie, D Slagstad, D Beare, J Dunn, et al. 1999. "Climate Fluctuations and the Spring Invasion of the North Sea by Calanus Finmarchicus." *Fisheries Oceanography* 8 (s1): 163–76. doi:10.1046/j.1365-2419.1999.00008.x.

Heath, Michael R., Peter R. Boyle, Astthor Gislason, William S.C. Gurney, Stephen J. Hay, Erica J.H. Head, Steven Holmes, et al. 2004. "Comparative Ecology of over-Wintering Calanus Finmarchicus in the Northern North Atlantic, and Implications for Life-Cycle Patterns." *ICES Journal of Marine Science* 61 (4): 698–708. doi:10.1016/j.icesjms.2004.03.013.

Hébert, Marie-Pier, Beatrix E. Beisner, and Roxane Maranger. 2016a. "A Meta-Analysis of Zooplankton Functional Traits Influencing Ecosystem Function." *Ecology* 97 (4): 1069–80. doi:10.1890/15-1084.1.

———. 2016b. "Linking Zooplankton Communities to Ecosystem Functioning: Toward an Effect-Trait Framework." *Journal of Plankton Research* 0: 1–10. doi:10.1093/plankt/fbw068.

Hinzman, Larry D., Clara J. Deal, A. David Mcguire, Sebastian H. Mernild, Igor V.

Polyakov, and John E. Walsh. 2013. “Trajectory of the Arctic as an Integrated System.” *Ecological Applications* 23 (8): 1837–68. doi:10.1890/11-1498.1.

Hirche, H.J. 1987. “Temperature and Plankton II: Effect on Respiration and Swimming Activity in Copepods from the Green Land Sea.” *Marine Biology* 94: 347–56.

Hirche, Hans.-Jürgen. 1996. “Diapause in the Marine Copepod, Calanus Finmarchicus - A Review.” *Ophelia* 44 (October): 129–43. doi:10.1080/00785326.1995.10429843.

Holland, M. M., and C. M. Bitz. 2003. “Polar Amplification of Climate Change in Coupled Models.” *Climate Dynamics* 21 (3–4): 221–32. doi:10.1007/s00382-003-0332-6.

Ikeda, T., and H. R. Skjoldal. 1989. “Metabolism and Elemental Composition of Zooplankton from the Barents Sea during Early Arctic Summer.” *Marine Biology* 100 (2): 173–83. doi:10.1007/BF00391956.

Ikeda, Tsutomu, Y. Kanno, K. Ozaki, and A. Shinada. 2001. “Metabolic Rates of Epipelagic Marine Copepods as a Function of Body Mass and Temperature.” *Marine Biology* 139 (5): 1020–1020. doi:10.1007/s002270100608.

Ji, Rubao, Meibing Jin, and Øystein Varpe. 2013. “Sea Ice Phenology and Timing of Primary Production Pulses in the Arctic Ocean.” *Global Change Biology* 19 (3): 734–41. doi:10.1111/gcb.12074.

Johannessen, Ola M., and Martin W. Miles. 2011. “Critical Vulnerabilities of Marine and Sea Ice-Based Ecosystems in the High Arctic.” *Regional Environmental Change* 11 (SUPPL. 1): 239–48. doi:10.1007/s10113-010-0186-5.

Johnson, Catherine L., Andrew W. Leising, Jeffrey A. Runge, Erica J H Head, Pierre Pepin, St??phane Plourde, and Edward G. Durbin. 2008. “Characteristics of Calanus Finmarchicus Dormancy Patterns in the Northwest Atlantic.” *ICES Journal of Marine Science* 65 (3): 339–50. doi:10.1093/icesjms/fsm171.

Joli, Nathalie, Adam Monier, Ramiro Logares, and Connie Lovejoy. 2017. “Seasonal Patterns in Arctic Prasinophytes and Inferred Ecology of Bathycoccus Unveiled in an Arctic Winter Metagenome.” *The ISME Journal* 11 (6): 1372–85. doi:10.1038/ismej.2017.7.

Jónasdóttir, Sigrún Huld, André W. Visser, Katherine Richardson, and Michael R Heath. 2015. “Seasonal Copepod Lipid Pump Promotes Carbon Sequestration in the Deep North Atlantic.” *Proceedings of the National Academy of Sciences of the United States of America* 112 (39): 12122–26. doi:10.1073/pnas.1512110112.

Kattner, G., W. Hagen, R.F. Lee, R. Campbell, D. Deibel, S. Falk-Petersen, M. Graeve, et al. 2007. “Perspectives on Marine Zooplankton Lipids.” *Canadian Journal of Fisheries and Aquatic Sciences* 1639: 1628–39. doi:10.1139/f07-122.

Kattner, Gerhard, and Hagen Wilhelm. 2009. “Lipids in Marine Copepods: Latitudinal Characteristics and Perspective to Global Warming.” *Lipids in Aquatic Ecosystems*, xv–xx. doi:10.1007/978-0-387-89366-2.

Kiørboe, Thomas, and George A Jackson. 2001. “Marine Snow, Organic Solute Plumes, and Optimal Chemosensory Behavior of Bacteria.” *Limnology and Oceanography* 46 (6): 1309–18. doi:10.4319/lo.2001.46.6.1309.

Kosobokova, Ksenia N., and Russell R. Hopcroft. 2010. “Diversity and Vertical Distribution of Mesozooplankton in the Arctic’s Canada Basin.” *Deep-Sea Research Part II: Topical Studies in Oceanography* 57 (1–2). Elsevier: 96–110. doi:10.1016/j.dsr2.2009.08.009.

Lee, R F, W Hagen, and G Kattner. 2006. “Lipid Storage in Marine Zooplankton.” *Marine Ecology Progress Series* 307 (1863): 273–306. doi:Doi 10.3354/Meps307273.

Leu, E., C. J. Mundy, P. Assmy, K. Campbell, T. M. Gabrielsen, M. Gosselin, T. Juul-

Pedersen, and R. Gradinger. 2015. “Arctic Spring Awakening - Steering Principles behind the Phenology of Vernal Ice Algal Blooms.” *Progress in Oceanography* 139. Elsevier Ltd: 151–70. doi:10.1016/j.pocean.2015.07.012.

Leu, E., J. E. Søreide, D. O. Hessen, S. Falk-Petersen, and J. Berge. 2011. “Consequences of Changing Sea-Ice Cover for Primary and Secondary Producers in the European Arctic Shelf Seas: Timing, Quantity, and Quality.” *Progress in Oceanography* 90 (1–4). Elsevier Ltd: 18–32. doi:10.1016/j.pocean.2011.02.004.

Lindsay, R. W., J. Zhang, A. Schweiger, M. Steele, and H. Stern. 2009. “Arctic Sea Ice Retreat in 2007 Follows Thinning Trend.” *Journal of Climate* 22 (1): 165–76. doi:10.1175/2008JCLI2521.1.

Maps, Frédéric, Nicholas R. Record, and Andrew J. Pershing. 2014. “A Metabolic Approach to Dormancy in Pelagic Copepods Helps Explaining Inter- and Intra-Specific Variability in Life-History Strategies.” *Journal of Plankton Research* 36 (1): 18–30. doi:10.1093/plankt/fbt100.

Maps, Frédéric, Jeffrey A. Runge, Andrew Leising, Andrew J. Pershing, Nicholas R. Record, Stéphane Plourde, and James J. Pierson. 2011. “Modelling the Timing and Duration of Dormancy in Populations of Calanus Finmarchicus from the Northwest Atlantic Shelf.” *Journal of Plankton Research* 34 (1): 36–54. doi:10.1093/plankt/fbr088.

Mariani, Patrizio, Ken H. Andersen, André W. Visser, Andrew D. Barton, and Thomas Kiørboe. 2013. “Control of Plankton Seasonal Succession by Adaptive Grazing.” *Limnology and Oceanography* 58 (1): 173–84. doi:10.4319/lo.2013.58.1.0173.

Marshall, S. M., and A. P. Orr. 1958. “On the Biology of Calanus Finmarchicus X. Seasonal Changes in Oxygen Consumption.” *Journal of the Marine Biological Association of the United Kingdom* 37 (2): 459. doi:10.1017/S002531540002381X.

Martin, Johannie, Dany Dumont, and Jean-Éric Tremblay. 2013. “Contribution of Subsurface Chlorophyll Maxima to Primary Production in the Coastal Beaufort Sea (Canadian Arctic): A Model Assessment.” *Journal of Geophysical Research: Oceans* 118 (11): 5873–86. doi:10.1002/2013JC008843.

Martin, Johannie, Jean-Éric Tremblay, Jonathan Gagnon, Geneviéve Tremblay, Amandine Lapoussiére, Caroline Jose, Michel Poulin, Michel Gosselin, Yves Gratton, and Christine Michel. 2010. “Prevalence, Structure and Properties of Subsurface Chlorophyll Maxima in Canadian Arctic Waters.” *Marine Ecology Progress Series* 412: 69–84. doi:10.3354/meps08666.

Martini, Kim I., Phyllis J. Stabeno, Carol Ladd, Peter Winsor, Thomas J. Weingartner, Calvin W. Mordy, and Lisa B. Eisner. 2016. “Dependence of Subsurface Chlorophyll on Seasonal Water Masses in the Chukchi Sea.” *Journal of Geophysical Research: Oceans* 121 (3): 1755–70. doi:10.1002/2015JC011359.

Mayzaud, P. 1976. “Respiration and Nitrogen Excretion of Zooplankton. IV. The Influence of Starvation on the Metabolism and the Biochemical Composition of Some Species.” *Marine Biology* 37 (1): 47–58. doi:10.1007/BF00386778.

Mayzaud, P, and Rj Conover. 1988. “O:N Atomic Ratio as a Tool to Describe Zooplankton Metabolism.” *Marine Ecology Progress Series* 45: 289–302. doi:10.3354/meps045289.

Menden-Deuer, Susanne, and Thomas Kiørboe. 2016. “Small Bugs with a Big Impact: Linking Plankton Ecology with Ecosystem Processes.” *Journal of Plankton Research*, no. August. doi:10.1093/plankt/fbw049.

Meunier, Cédric L., Maarten Boersma, Karen H. Wiltshire, and Arne M. Malzahn. 2016. “Zooplankton Eat What They Need: Copepod Selective Feeding and Potential

Consequences for Marine Systems.” *Oikos* 125 (1): 50–58. doi:10.1111/oik.02072.

Michel, C, L. Legendre, R G Ingram, M Gosselin, and M Levasseur. 1996. “Carbon Budget of Sea-Ice Algae in Spring: Evidence of a Significant Transfer to Zooplankton Grazers.” *Journal of Geophysical Research: Oceans* 101 (C8): 18345–60. doi:10.1029/96JC00045.

Mitra, Aditee, Claudia Castellani, Wendy C Gentleman, Sigrún H Jónasdóttir, Kevin J Flynn, Antonio Bode, Claudia Halsband, et al. 2014. “Progress in Oceanography Bridging the Gap between Marine Biogeochemical and Fisheries Sciences ; Configuring the Zooplankton Link.” *Progress in Oceanography* 129. Elsevier Ltd: 176–99. doi:10.1016/j.pocean.2014.04.025.

Mitra, Aditee, and Kevin J. Flynn. 2005. “Predator–prey Interactions: Is ‘ecological Stoichiometry’ Sufficient When Good Food Goes Bad?” *Journal of Plankton Research* 27 (5): 393–99. doi:10.1093/plankt/fbi022.

Mitra, Aditee, Kevin J. Flynn, and Michael J. R. Fasham. 2007. “Accounting for Grazing Dynamics in Nitrogen-Phytoplankton-Zooplankton (NPZ) Models.” *Limnology and Oceanography* 52 (2): 649–61. doi:10.4319/lo.2007.52.2.0649.

Moloney, Coleen L., and John G. Field. 1989. “General Allometric Equations for Rates of Nutrient Uptake, Ingestion, and Respiration in Plankton Organisms.” *Limnology and Oceanography* 34 (7): 1290–99. doi:10.4319/lo.1989.34.7.1290.

Ohman, Mark D., Aleksandr V. Drits, M. Elizabeth Clarke, and Stéphane Plourde. 1998. “Differential Dormancy of Co-Occurring Copepods.” *Deep-Sea Research Part II: Topical Studies in Oceanography* 45 (8–9): 1709–40. doi:10.1016/S0967-0645(98)80014-3.

Olli, Kalle, Paul Wassmann, Marit Reigstad, Tatjana N. Ratkova, Elena Arashkevich, Anna Pasternak, Patricia A. Matrai, et al. 2007. “The Fate of Production in the Central Arctic Ocean - Top-down Regulation by Zooplankton Expatriates?” *Progress in Oceanography* 72 (1): 84–113. doi:10.1016/j.pocean.2006.08.002.

Overland, James E., and Muyin Wang. 2013. “When Will the Summer Arctic Be Nearly Sea Ice Free?” *Geophysical Research Letters* 40 (10): 2097–2101. doi:10.1002/grl.50316.

Palmer, Molly A., Kevin R. Arrigo, C. J. Mundy, Jens K. Ehn, Michel Gosselin, David G. Barber, Johannie Martin, Eva Alou, Suzanne Roy, and Jean Éric Tremblay. 2011. “Spatial and Temporal Variation of Photosynthetic Parameters in Natural Phytoplankton Assemblages in the Beaufort Sea, Canadian Arctic.” *Polar Biology* 34 (12): 1915–28. doi:10.1007/s00300-011-1050-x.

Polyakov, Igor V., Uma S. Bhatt, John E. Walsh, E. Povl Abrahamsen, Andrey V. Pnyushkov, and Paul F. Wassmann. 2013. “Recent Oceanic Changes in the Arctic in the Context of Long-Term Observations.” *Ecological Applications* 23 (8): 1745–64. doi:10.1890/11-0902.1.

Prowe, A. E Friederike, Markus Pahlow, Stephanie Dutkiewicz, Michael Follows, and Andreas Oschlies. 2012. “Top-down Control of Marine Phytoplankton Diversity in a Global Ecosystem Model.” *Progress in Oceanography* 101 (1). Elsevier Ltd: 1–13. doi:10.1016/j.pocean.2011.11.016.

Sommer, Ulrich, Rita Adrian, Lisette De Senerpont Domis, James J. Elser, Ursula Gaedke, Bas Ibelings, Erik Jeppesen, et al. 2011. “Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession.” *Annual Review of Ecology, Evolution, and Systematics* 43 (1): 120913143848009. doi:10.1146/annurev-ecolsys-110411-160251.

Steinberg, Deborah K., and Michael R. Landry. 2017. "Zooplankton and the Ocean Carbon Cycle," no. October 2016: 1–32. doi:10.1146/annurev-marine-010814-015924.

Stocker, Thomas, Gian-Kasper Plattner, Melinda Tignor, Simon Allen, Judith Boschung, Alexander Nauels, Yu Xia, Vincent Bex, and Pauline Midgley. 2013. *Climate Change 2013 - The Physical Science Basis*. Edited by Intergovernmental Panel on Climate Change. *Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5)(Cambridge Univ Press, New York)*. Cambridge: Cambridge University Press. doi:10.1017/CBO9781107415324.

Sunda, W. G., and D. R. Hardison. 2010. "Evolutionary Tradeoffs among Nutrient Acquisition, Cell Size, and Grazing Defense in Marine Phytoplankton Promote Ecosystem Stability." *Marine Ecology Progress Series* 401 (Cloern 2001): 63–76. doi:10.3354/meps08390.

Talmy, D., J. Blackford, N. J. Hardman-Mountford, L. Polimene, M. J. Follows, and R. J. Geider. 2014. "Flexible C : N Ratio Enhances Metabolism of Large Phytoplankton When Resource Supply Is Intermittent." *Biogeosciences* 11 (17): 4881–95. doi:10.5194/bg-11-4881-2014.

Tande, K. S., and R. J. Henderson. 1988. "Lipid Composition of Copepodite Stages and Adult Females of Calanus Glacialis in Arctic Waters of the Barents Sea." *Polar Biology* 8 (5): 333–39. doi:10.1007/BF00442024.

Tande, Kurt S. 1982. "Ecological Investigations on the Zooplankton Community of Balsfjorden, Northern Norway: Generation Cycles, and Variations in Body Weight and Body Content of Carbon and Nitrogen Related to Overwintering and Reproduction in the Copepod Calanus Finmarchicus ." *Journal of Experimental Marine Biology and Ecology* 62 (2): 129–42. doi:10.1016/0022-0981(82)90087-9.

Tarrant, Ann M., Mark F. Baumgartner, Nadine S. J. Lysiak, Dag Altin, Trond R. Størseth, and Bjørn Henrik Hansen. 2016. "Transcriptional Profiling of Metabolic Transitions during Development and Diapause Preparation in the Copepod *Calanus Finmarchicus*." *Integrative and Comparative Biology*, icw060. doi:10.1093/icb/icw060.

Thor, Peter. 2000. "Relationship between Specific Dynamic Action and Protein Deposition in Calanoid Copepods." *Journal of Experimental Marine Biology and Ecology* 245 (2): 171–82. doi:10.1016/S0022-0981(99)00159-8.

———. 2002. "Specific Dynamic Action and Carbon Incorporation in Calanus Finmarchicus Copepodites and Females." *Journal of Experimental Marine Biology and Ecology* 272 (2): 159–69. doi:10.1016/S0022-0981(02)00131-4.

Tremblay, Jean-Éric, Leif G. Anderson, Patricia Matrai, Pierre Coupel, Simon Bélanger, Christine Michel, and Marit Reigstad. 2015a. "Global and Regional Drivers of Nutrient Supply, Primary Production and CO2 Drawdown in the Changing Arctic Ocean." *Progress in Oceanography* 139: 171–96. doi:10.1016/j.pocean.2015.08.009.

———. 2015b. "Global and Regional Drivers of Nutrient Supply, Primary Production and CO2 Drawdown in the Changing Arctic Ocean." *Progress in Oceanography*. Elsevier Ltd. doi:10.1016/j.pocean.2015.08.009.

Tremblay, Jean-Éric, S Bélanger, D G Barber, M Asplin, J Martin, G Darnis, L Fortier, et al. 2011. "Climate Forcing Multiplies Biological Productivity in the Coastal Arctic Ocean." *Geophysical Research Letters* 38 (18): 2–6. doi:10.1029/2011GL048825.

Tremblay, Jean-Éric, and Jonathan Gagnon. 2009. "The Effects of Irradiance and Nutrient Supply on the Productivity of Arctic Waters: A Perspective on Climate Change." *Influence of Climate Change on the Changing Arctic and Sub-Arctic Conditions*, no.

Acia 2005: 73–93. doi:10.1007/978-1-4020-9460-6_7.

Tremblay, Jean-Éric, Dominique Robert, Diana E. Varela, Connie Lovejoy, Gérald Darnis, R. John Nelson, and Akash R. Sastri. 2012. "Current State and Trends in Canadian Arctic Marine Ecosystems: I. Primary Production." *Climatic Change* 115 (1): 161–78. doi:10.1007/s10584-012-0496-3.

Turner, Jefferson T. 2004. "The Importance of Small Pelagic Planktonic Copepods and Their Role in Pelagic Marine Food Webs." *Zoological Studies*.

Vanni, Michael J., and Peter B. McIntyre. 2016. "Predicting Nutrient Excretion of Aquatic Animals with Metabolic Ecology and Ecological Stoichiometry: A Global Synthesis." *Ecology*. doi:10.1002/ecy.1582.

Visser, Andre W., Josephine Grønning, and Sigrún Huld Jónasdóttir. 2017. "*Calanus Hyperboreus* and the Lipid Pump." *Limnology and Oceanography*, 1–15. doi:10.1002/lno.10492.

Walsh, John E., William L. Chapman, Vladimir Romanovsky, Jens H. Christensen, and Martin Stendel. 2008. "Global Climate Model Performance over Alaska and Greenland." *Journal of Climate* 21 (23): 6156–74. doi:10.1175/2008JCLI2163.1.

Wang, Muyin, and James E. Overland. 2012. "A Sea Ice Free Summer Arctic within 30 Years: An Update from CMIP5 Models." *Geophysical Research Letters* 39 (17): 6–11. doi:10.1029/2012GL052868.

Wang, Yanqing, Chaolun Li, Mengtan Liu, and Xin Jin. 2016. "Lipids and Fatty Acids in Calanus Sinicus during over-Summering in the Southern Yellow Sea." *Chinese Journal of Oceanology and Limnology*, no. 2011(September). doi:10.1007/s00343-017-5351-y.

Ward, B. A., S. Dutkiewicz, and M. J. Follows. 2014. "Modelling Spatial and Temporal Patterns in Size-Structured Marine Plankton Communities: Top-down and Bottom-up Controls." *Journal of Plankton Research* 36 (1): 31–47. doi:10.1093/plankt/fbt097.

Ward, B. a., S. Dutkiewicz, O. Jahn, and M. J. Follows. 2012a. "A Size-Structured Food-Web Model for the Global Ocean." *Limnology and Oceanography* 57 (6): 1877–91. doi:10.4319/lo.2012.57.6.1877.

———. 2012b. "A Size-Structured Food-Web Model for the Global Ocean." *Limnology and Oceanography* 57 (6): 1877–91. doi:10.4319/lo.2012.57.6.1877.

Wassmann, Paul. 2011. "Arctic Marine Ecosystems in an Era of Rapid Climate Change." *Progress in Oceanography* 90 (1–4): 1–17. doi:10.1016/j.pocean.2011.02.002.

Wassmann, Paul, Tatjana Ratkova, and Marit Reigstad. 2005. "The Contribution of Single and Colonial Cells of Phaeocystis Pouchetii to Spring and Summer Blooms in the North-Eastern North Atlantic." *Harmful Algae* 4 (5): 823–40. doi:10.1016/j.hal.2004.12.009.

Wassmann, Paul, and Marit Reigstad. 2011. "Future Arctic Ocean Seasonal Ice Zones and Implications for Pelagic-Benthic Coupling." *Oceanography* 24 (3): 220–31. doi:10.5670/oceanog.2011.74.

Waters, Colin N, Jan Zalasiewicz, Colin Summerhayes, Anthony D Barnosky, Clément Poirier, Agnieszka Ga, Alejandro Cearreta, et al. 2016. "The Anthropocene Is Functionally and Stratigraphically Distinct from the Holocene." *Science* 351 (6269): aad2622-1-aad2622-10. doi:10.1126/science.aad2622.