Université du Québec
à Rimouski

Effet de la température sur les taux physiologiques de la mye tronquée, *Mya truncata*

Mémoire présenté

dans le cadre du programme de maîtrise en océanographie

en vue de l'obtention du grade de maître ès sciences

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[Février 2024]

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Dépôt initial le 14 août 2023 Dépôt final le 8 février 2024

REMERCIEMENTS

J’aimerai remercier mon équipe de direction incroyable, David Deslauriers, Fanny Noisette et Chris McKindsey, pour leur mentorat et leur patience. Merci à Daniel Small pour son aide et ses contributions indispensables. Merci à ma technicienne Sarah-Maude Gagnon. Je remercie l’équipe de plongeurs à IML pour les myes, ainsi que tous les membres du projet de la Baie d’Hudson. Enfin, j’aimerai remercier ma famille et mes amis pour leur soutien sans fin pendant ce processus.

RÉSUMÉ

L'Arctique canadien subit des grandes transformations dues aux changements climatiques, notamment un réchauffement jusqu'à deux fois plus rapide et important qu'observé ailleurs sur la planète. Cela entraine une réduction de la formation de glace qui risque d'avoir un impact sur le fonctionnement des écosystèmes dont les compartiments benthiques et pélagiques sont fortement liés. La mye tronquée, *Mya truncata*, apporte une très grande contribution à la structure de plusieurs écosystèmes arctiques où elle est trouvée en grande densité. Comme suspensivore, cette espèce de bivalve vivant dans les substrats meubles, crée un lien direct entre la production primaire de surface et les mammifères marins dont elle est la proie, renforçant le couplage bentho-pélagique dans ces environnements. Jusqu'à maintenant, le manque flagrant d'information sur l'impact de la température sur cette espèce rendait difficile les prédictions quant à son devenir dans un contexte de réchauffement rapide de l'Arctique. L'objectif de ce projet est d'évaluer l'impact de la température sur les taux physiologiques de la mye tronquée pour mieux comprendre les effets possibles du réchauffement sur cette espèce. Le taux de filtration, la consommation d'oxygène, l'excrétion d'ammonium et la calcification ont été mesurés à cinq températures retrouvées actuellement et dans le futur dans l'habitat de la mye (5, 7, 11, 14, 17 °C). Seule la consommation d'oxygène a montré une tendance d'augmentation avec une augmentation de température. Les autres taux n'ont pas été influencés par l'augmentation de la température. La population provenant de l'estuaire du Saint-Laurent, qui se situe vers le sud de l'aire de répartition de cette espèce, semble s'approcher de sa limite thermique à 17 °C. Ces informations nous permettent donc une meilleure compréhension de la physiologie de la mye tronquée afin de nous éclairer sur les conséquences potentielles du réchauffement global sur cette espèce ainsi que son rôle dans les écosystèmes arctiques.

Mots clés : Changement climatique, Écophysiologie, Tolérance thermique

ABSTRACT

The Canadian Arctic is currently experiencing major transformations due to climate change, notably, amplified warming that is up to two times the temperature increase observed globally. This warming leads to decreased ice cover, which may impact the functioning of ecosystems for which the benthic and pelagic compartments are tightly linked. The truncate soft-shell clam, *Mya truncata*, provides an important contribution to the structure of many Arctic ecosystems. As a filter feeder, this species which lives in loose sediment, creates a direct link between primary producers and marine mammals and can be found at high densities in certain Arctic regions. Until now, the glaring lack of information on the impact of temperature on this species makes it difficult to predict its future in the rapidly warming Arctic. The objective of this project is to evaluate the impact of temperature on different physiological rates of *M. truncata* to further our understanding of the potential effects of warming on this species. Filtration, oxygen consumption, ammonium excretion and calcification rates were measured at five temperatures found in the clam's current and future habitats (5, 7, 11, 14, 17 °C). Only oxygen consumption showed an increasing trend with increasing temperature. The other rates were not influenced by temperature. The Saint Lawrence Estuary population, near the southern edge of this species' distribution, seemed to approach its upper thermal limit at 17 °C. This information allows us to better understand the physiology of *M. truncata* and enlightens us to the potential consequences global warming can have on this species as well as its role in Arctic ecosystems.

Keywords: Climate change, Ecophysiology, Thermal tolerance

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

INTRODUCTION GÉNÉRALE

1.1 LES CHANGEMENTS CLIMATIQUES DANS LES ÉCOSYSTÈMES ARCTIQUES

L'Arctique canadien subit présentement de grandes transformations dues aux conséquences des changements climatiques. À cause des périodes plus longues sans glace, la surface de l'eau absorbe plus de radiation, ce qui a pour effet d'amplifier la magnitude du réchauffement par, en moyenne, deux fois le taux observé mondialement (Stewart et Lockhart 2005, Hamilton 2013). La baie d'Hudson est une région subarctique, mais qui reflète les caractéristiques de l'Arctique (Hoover et al. 2013a). Dans la baie d'Hudson, Lavoie et al. (2013) prédisent que la température de surface moyenne va augmenter jusqu'à 0.31 ± 0.07 °C par décennie, et une formation de glace plus tard et une fonte plus tôt qui résulteraient en jusqu'à trois mois moins de couvert de glace. La diminution de la présence de glace et l'augmentation de la température risquent d'avoir un impact sur la structure et le fonctionnement des écosystèmes arctiques de la baie d'Hudson (Stewart et Lockhart 2005). Effectivement, les algues de glace, algues qui se forme sous la glace au début printemps, sont à la base du régime alimentaire de plusieurs organismes benthiques filtreurs dans la baie d'Hudson, notamment quand les concentrations de phytoplancton sont faibles en hiver (Hoover et al. 2013a), générant ainsi un fort couplage pélago-benthique. Avec la diminution de glace, le système subit une évolution vers un système dominé par la production pélagique phytoplanctonique et un déclin en organismes benthiques (Hoover et al. 2013a). En effet, le sud de la baie d'Hudson et la baie James sont caractérisés par une grande entrée d'eau douce de rivières et de la fonte de glace qui s'accumule à cause de forts vents du nord-ouest (Stewart et Lockhart 2005). Cela crée une forte stratification qui entraine une augmentation exagérée de la couche de surface isolée du reste de la colonne d'eau et rend difficile le transport de la production planctonique de surface vers les écosystèmes benthiques (Stewart et Lockhart

2005). Les changements climatiques, comme l'augmentation de la température et les changements en salinité et pH risquent de perturber le fonctionnement des écosystèmes dont les compartiments benthiques et pélagiques sont fortement liés.

Les systèmes arctiques démontrent un fort couplage pélago-benthique et leur fonctionnement se base sur le concept de voies énergétiques (McMeans et al. 2013). Rooney et al. (2006) décrit la présence de différentes voies d'énergie qui déterminent la stabilité et résilience des réseaux trophiques. Les voies sont des chaines trophiques qui redirigent l'énergie à partir de différentes sources de carbone. Dans des systèmes aquatiques, le carbone provient, en général, soit du phytoplancton dans la zone pélagique ou du détritus dans la zone benthique, qui représentent leur propre dynamique énergétique (Rooney et al. 2006). La présence de plusieurs voies énergétiques augment la capacité d'un écosystème à rétablir un état d'équilibre après une perturbation. Les changements engendrés par une augmentation de température et surtout une diminution de présence de glace, risquent de perturber cet équilibre. Une diminution de glace mène à une plus haute disponibilité de lumière et plus de production primaire dans la zone pélagique. Les conséquences de cette augmentation de production pélagique pour le benthos ne font pas consensus. Dans le détroit de Young au nord-est du Groenland, Sejr et Christensen (2007) ont prédit que la diminution de glace serait bénéfique aux organismes benthiques qui sont normalement limités par la disponibilité de nourriture. À l'opposé, un modèle Ecopath avec Ecosim de la baie d'Hudson prédit une diminution de l'abondance des organismes benthiques due à une diminution de détritus provenant des algues de glaces (Hoover et al. 2013b). Cette tendance vers un diminution de l'abondance des organismes benthiques a déjà eu lieu au nord de la mer de Béring (Grebmeier et al. 2006). Habituellement, il y a une exportation importante de carbone pélagique non-consommé vers le benthos dans l'arctique qui alimente les organismes benthiques. Grebmeier et al. (2006) ont démontré une diminution d'approvisionnement de carbone vers le benthos, associé avec une diminution du stock benthique de 40 g C m^{-2} à 20 g C m^{-2} entre 1988 et 2004 au nord de la mer de Béring. Une diminution de la biomasse benthique pourrait perturber la stabilité de l'écosystème. En effet, les bivalves suspensivores jouent un rôle indispensable dans le couplage pélago-benthique en filtrant la colonne d'eau et en

concentrant la matière organique au niveau du sédiment (Newell 2004). Un des bivalves importants à travers les écosystèmes arctiques est la mye tronquée, *Mya truncata* (Welch et al. 1992). Due à sa vie sédentaire et à sa grande longévité, elle est une bonne espèce indicatrice pour étudier l'effet des changements climatiques sur l'écosystème de la baie d'Hudson (Schaefer et al. 2021).

1.2 LA TEMPÉRATURE

La température est un facteur important qui détermine la distribution géographique de la majorité des organismes ectothermes (Pörtner 2002). La température détermine les réactions chimiques et donc le fonctionnement des taux physiologiques. Cependant, la communité scientifique reste divisée sur les mécanismes qui sous-tendent la tolérance thermique. Le paradigme de Fry est un modèle conceptuel qui décrit l'influence de facteurs environnementaux sur le registre aérobie d'un organisme (Fry 1971). Le registre aérobie est la différence entre le taux métabolique maximal (le taux métabolique le plus élevé qu'un organisme peut atteindre) et le taux métabolique standard (l'énergie qui est requise pour la maintenance somatique de base et la survie à une température donnée). Le registre aérobie représente donc l'énergie disponible pour toutes activités au-delà du maintien, comme la locomotion, la digestion, la reproduction et la croissance des tissus. Selon le paradigme de Fry (Fig 1), pour les ectothermes, quand la température augmente, le taux métabolique standard augmente de manière exponentielle due à l'effet direct de la température sur le fonctionnement enzymatique, et le taux métabolique maximal augmente avant d'atteindre un plateau à la limite de la capacité aérobie de l'organisme puis à ensuite tendance à chuter. Cela résulte en un registre aérobie qui augmente jusqu'à un maximum et qui ensuite diminue quand le taux métabolique standard consomme une fraction plus grande de la capacité métabolique totale (Fry 1971). Pörtner et al. (2017) propose l'hypothèse de l'« oxygen- and capacity- limited thermal tolerance » (OCLTT), qui déclare que la courbe de performance décrite par Fry est basée sur la capacité d'un organisme à fournir l'oxygène aux tissus. À

basses températures, les organismes ont une capacité réduite d'utilisation d'oxygène due au fonctionnement limité des enzymes à ces températures, et à des hautes températures le système cardiorespiratoire ne peut fournir l'oxygène requis pour maintenir des taux métaboliques élevés (Pörtner et al. 2017). Cette théorie tente de créer un lien entre la recherche physiologique et écologique et d'intégrer plusieurs niveaux d'organisation biologiques. L'intégration de mécanismes moléculaires jusqu'à l'organisme entier est nécessaire pour mieux comprendre les contraintes thermiques pour la distribution géographique des espèces et les implications au niveau de l'écosystème (Pörtner et al. 2017).

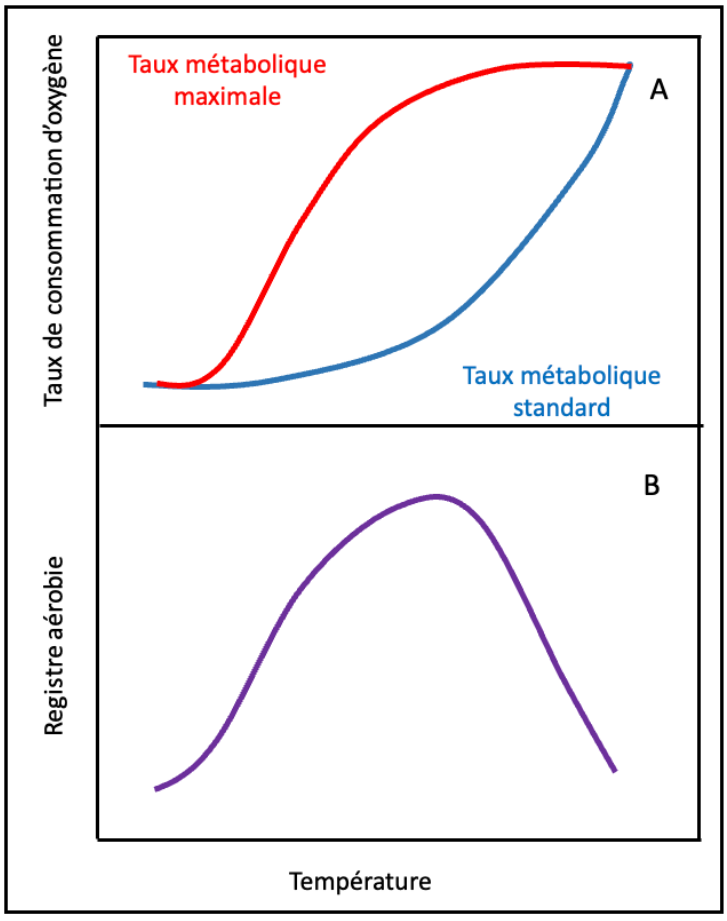


Figure 1. Un modèle conceptuel du paradigme de Fry (Fry 1971 ; modifié de McKenzie et al. 2016). Les lignes bleues et rouges dans (A) modélisent le taux métabolique standard (minimal; SMR) et le taux métabolique maximal (MMR) variant en fonction de la

température. La différence entre SMR et MMR est la registre aérobie (B) qui forme une courbe de performance claire en forme de cloche.

Cependant, l'OCLTT est difficile à valider et n'est pas forcément valable pour toutes les espèces (Schulte 2015). Plusieurs auteurs remettent en question cette hypothèse qui manque de données pour valider les interprétations (Jutfelt et al. 2018). En premier lieu, l'hypothèse OCLTT et le paradigme de Fry présument que la performance et l'aptitude biologique d'un organisme sont liées directement au registre aérobie et que la température optimale pour l'aptitude biologique est la même température qui corresponde au moment où le registre aérobie est le plus grand. En revanche, des études ont trouvé que les températures optimales pour la croissance et pour la reproduction ne correspondent pas à la température optimale pour le registre aérobie, ce qui suggère que différentes fonctions physiologiques ont des optimums de température différents (Clark et al. 2013, Schulte 2015). De plus, la forme de cloche des courbes de performance thermique proposée par Fry et l'OCLTT n'est pas aussi universelle que suggérée. Munday et al. (2009) ont démontré que le registre aérobie reste grand jusqu'à près de la limite létale et suggère que la limitation d'oxygène prend effet seulement à des températures létales. Malgré le débat en cours, les limites thermiques demeurent des indicateurs importants pour évaluer l'effet des stresseurs environnementaux (McKenzie et al. 2016). Une stresseur est quelque chose qui menace l'homéostasie d'un organisme et entraine une série complexe de réponses adaptives afin de ré-établir cette homéostasie (Schulte 2014). La compréhension fondamentale des mécanismes associés aux limites thermiques est cruciale pour mieux comprendre les effets des changements climatiques sur les écosystèmes marins.

L'une des méthodes pour comprendre les effets des changements climatiques est d'utiliser des modèles de distribution d'espèces pour en prédire les changements attendus (Teal et al. 2018). Jusqu'à récemment, ces modèles utilisaient des données de présence et absence et de conditions environnementales actuelles pour prédire une distribution sous contrainte de changements environnementaux (Teal et al. 2018). Cependant, cette approche appliquée à la gestion de la conservation essaie d'extrapoler des données de présence dans

des régions hors des données historiques de présence d'espèce. De plus, les réponses d'une espèce aux changements environnementaux sont complexes et les données de présence/absence prennent forcément en compte des interactions prédateur/proie et des limites de dispersion qui ne sont pas considérées dans les extrapolations. Une approche plus mécanistique pour prédire la distribution future d'une espèce est d'utiliser des modèles basés sur la physiologie, car les processus physiologiques sont à la base de la réponse d'un organisme face à son environnement (Pörtner 2002, Claireaux et Lefrançois 2007, Teal et al. 2018). L'un de ces modèles possibles est le Dynamic Energy Budget (DEB) qui est un modèle bioénergétique qui prend en compte l'apport et l'utilisation d'énergie dans un organisme et l'influence de la température et la disponibilité de nourriture (Kooijman 2000). Chaque type de modèle se base sur des suppositions pour pouvoir modéliser les processus complexes du fonctionnement d'un organisme. L'une des suppositions importantes du DEB est que tous les taux physiologiques ont la même réponse à la température (Kooijman 2000). En revanche, même si la plupart des taux physiologiques augmentent avec une augmentation de la température, la forme des courbes de réponses peut varier. La forme d'une courbe de performance thermique dépend des processus biochimiques qui gouvernent la fonction considérée (Schulte et al. 2011). Cela peut entrainer plusieurs courbes de performance thermique au niveau de l'organisme entier (Schulte et al. 2011). Pour l'huitre *Ostrea edulis*, le taux de filtration maximal était observé à 15 °C, mais la consommation d'oxygène était constante entre 5 et 20 °C avec un augmentation rapide à 25 °C. La moule *Modiolus barbatus* présente une augmentation des taux de filtration entre 9 et 28 °C, tandis que la consommation d'oxygène était la plus élevée aux basses températures (Ezgeta-Balić et al. 2011). Il est ainsi important d'acquérir des données empiriques de courbes de performance thermique pour différents taux physiologiques afin de paramétrer correctement les modèles énergétiques informant les prédictions face aux changements climatiques.

Toutefois, la vulnérabilité thermique des organismes dans le contexte des changements climatiques demeure un sujet de recherche compliqué à cause de la plasticité des taux physiologiques au sein et parmi les générations (Magozzi et Calosi 2015). L'hypothèse de variabilité climatique propose que les organismes dans les environnements

variables aient une large fenêtre de tolérance thermique ce qui contraste avec les organismes dans les climats plus constants qui auront des tolérances plus restreintes (Compton et al. 2007). Les variations de températures ambiantes pourraient également avoir un effet sur la sensibilité des taux physiologiques. Un haut degré de sensibilité thermique signifie qu'un petit changement de température résulte dans un réponse physiologique importante étant donné qu'une faible sensibilité suggère une faible réponse physiologique (Gilchrist 2000). La sensibilité thermique a une base enzymatique qui suggère un compromis entre l'efficacité catalytique et l'ampleur thermique. Les espèces adaptées aux environnements froides sont en générales plus sensibles aux augmentations de température (Gilchrist 2000). La température d'Arrhenius (T_A) est une mesure de la sensibilité d'un taux physiologique aux changements de température. Cette mesure est utile parce qu'elle permette de standardiser et de comparer la variation des taux en fonction de la température avec la littérature. T_A est une approximation des réactions biomoléculaires dans la phase gazeuse (Glasstone et al. 1941). Elle peut justement être utilisée pour calculer l'énergie d'activation des enzymes (Kooijman 2000).

1.3 LA MYE TRONQUÉE

La mye tronquée, *Mya truncata*, est une espèce boréal-arctique qui est retrouvée dans une grande diversité de substrats sédimentaires comme le sable, la vase et le gravier (Hewitt et Dale 1984, Amaro et al. 2003). Sa distribution s'étend de la baie du Massachusetts (42 °N) jusqu'au haut Arctique. Il a été proposé que *M. truncata* représente un complexe d'espèces et non une seule espèce, mais des spécimens de toute sa distribution ainsi que plus de données comme la « spermatozoan ultramorphology » seront importants pour être certain de son statut taxonomique (Petersen 1999, Zhang et al. 2018). *Mya truncata*, comme plusieurs autres organismes polaires, est longévive et possède un lent taux de croissance (Hewitt et Dale 1984, Amaro et al. 2003, Witbaard et al. 2005, Sejr et Christensen 2007). L'âge de *M. truncata* peut être déterminé par les bandes de croissance à l'intérieur du chondrophore, une structure

interne près de la charnière à laquelle se fixe le ligament interne chez certaines bivalves (MacDonald et Thomas 1980, Hewitt et Dale 1984). Elles peuvent atteindre un âge maximal de 62 ans (Siferd 2005), mais l'âge maximal ainsi que les taux de croissance dépendent fortement des conditions environnementales à l'endroit de l'étude (Hewitt et Dale 1984, Witbaard et al. 2005). Le taux de croissance diminue avec l'âge (Hewitt et Dale 1984, Amaro et al. 2003, Vieweg et al. 2012). *Mya truncata* est une espèce diœcique qui se reproduit par expulsion des gamètes des deux sexes dans le milieu, et la période de reproduction peut fortement varier entre les différentes régions. Hewitt et Dale (1984) ont observé une période de reproduction entre mai et le début de juillet, après la débâcle de glace au Groenland. En d'autres régions du Groenland, *Mya truncata* peuvent pondre pendant toute l'année (Petersen 1978). Brandner et al. (2017) indiquent qu'elles ont plusieurs périodes de reproduction à Adventfjorden, Svalbard, une au printemps et une à l'automne. Cette espèce se disperse au stade de larve pélagique, processus qui est fortement influencé par les conditions hydrographiques locales (Hewitt et Dale 1984, Schlüter et Rachor 2001). La latitude semble avoir un effet sur la durée de vie larvaire dans la colonne d'eau, avec une diminution de 5 à 2 mois aux latitudes plus basses (Brandner et al. 2017). L'abondance des larves est corrélée avec la concentration de chlorophylle a plutôt qu'avec la température ce qui suggère que la disponibilité de nourriture est l'un des facteurs majeurs qui influence la ponte (Brandner et al. 2017).

Mya truncata est une espèce benthique dominante dans plusieurs régions arctiques, et peut atteindre des densités de 136 individus m^{-2} dans le détroit de Lancaster (Welch et al. 1992, Sejr et Christensen 2007). Elles se retrouvent principalement dans les eaux peu profondes, jusqu'à 80 m, mais préfèrent des eaux moins profondes avec les plus hautes densités vers 30 m (Petersen 1978, Welch et al. 1992, Sejr et Christensen 2007). La disponibilité de nourriture semble être le facteur principal qui limite la distribution en profondeur (Sejr et Christensen 2007). Due à ses densités élevées à travers l'Arctique, *M. truncata* joue un rôle important dans le flux d'énergie et le cycle du carbone dans les écosystèmes arctiques (Welch et al. 1992). Elles se nourrissent par filtration, ce qui augmente la sédimentation et aide à concentrer la matière organique au niveau du benthos en y déposant

le carbone qui n'est pas assimilé en forme de fèces et pseudofèces dans le sédiment (Welch et al. 1992, Sejr et Christensen 2007). Une analyse des acides gras suggère que la matière organique particulaire du sédiment compose une partie importante de la diète de *M. truncata* pendant l'hiver dans le sud-ouest de la baie de Baffin venant compléter les particules en provenance de la colonne d'eau (Amiraux et al. 2021). Cette supplémentation de la diète permet une source de nourriture plus constante pendant l'année, mais est pauvre en acides gras essentiels. De plus, *M. truncata* permet un lien trophique direct entre les producteurs primaires et les mammifères marins (Sejr et Christensen 2007). En effet, *M. truncata* constitue une partie importante de la diète des morses (*Odobenus rosmarus*), représentant jusqu'à 81.4% de l'énergie brute totale consommée par les morses dans le nord du bassin de Foxe (Welch and Martin-Bergmann 1990, Fisher et Stewart 1997, Born et al. 2003). Les restants des myes non-consommés par ces prédateurs supérieurs sont rapidement consommés par des charognards comme les amphipodes lysianassid et les buccins (*Buccinum spp*.) (Welch et Martin-Bergmann 1990). L'importance de *M. truncata* dans le transfert d'énergie à travers les écosystèmes arctiques est reconnue : l'espèce est considérée dans plusieurs études portant sur les contaminants et notamment pour leur rôle dans la biomagnification à travers le réseau trophique (Bright et al. 1995, Fisk et al. 2003, Tomy et al. 2004).

En plus de son importance écologique, *M. truncata* est importante pour les communautés Inuites comme nourriture de subsistance. Non seulement la nourriture de subsistance offre une source de nutriments importante, mais elle représente un aspect intégral de la culture Inuite qui fournit aux communautés la sécurité d'un système économique solide (Wenzel 2009, Rapinski et al. 2018). Les changements climatiques exercent une influence sur leurs traditions. La chasse devient de plus en plus dangereuse avec les conditions environnementales qui sont moins prévisibles, des tempêtes et l'amincissement de la couche de glace sont propices à plus d'accidents et noyades (Furgal et Seguin 2006). Cependant, les Inuits sont un peuple qui ont une grande capacité d'adaptation (Furgal et Seguin 2006; Wenzel 2009). Les organismes intertidaux sont une ressource souvent oubliée dans la littérature (Rapinski et al. 2018) mais qui demeure importante pour plusieurs communautés Inuites. La récolte des organismes intertidaux offre plusieurs avantages : leur proximité, leur

abondance et accessibilité toute l'année, et l'absence d'équipement spécialisé pour les récolter (Rapinski et al. 2018). Des aînés font référence aux organismes intertidaux comme nourriture de famine. *Mya truncata* a été mentionnée par tous les participants d'une enquête de deux différentes communités Inuites au Nunavik comme une ressource récoltée, et un ainé l'a classifiée parmi les meilleurs trois organismes à manger avec *Alaria esculenta* et *Mytilus trossulus* (Rapinski et al. 2018). Le Nunavut Coastal Resource Inventory (NCRI 2008) fait référence à la consommation de *M. truncata* dans plusieurs communités au Nunavut également. Avec les conditions de glace qui deviennent moins prévisibles, les Inuits ont besoin de compenser pour les changements en accessibilité de poissons et mammifères marins. Les organismes intertidaux, comme la *M. truncata*, peuvent devenir une source fiable et même prenant de plus en plus d'importance pour les communités Inuites qui comptent en grande partie sur les ressources marines pour leur survie.

1.4 MON PROJET

Ce projet s'insère dans un plus grand projet (Hudson Bay Complex Results Fund) financé par Pêches et Océans Canada pour évaluer la résilience de l'écosystème de la Baie d'Hudson face aux changements climatiques. Le but du projet est de mieux comprendre l'effet des changements climatiques sur l'écosystème en évaluant l'effet de la température à plusieurs niveaux d'organisation biologique et à travers plusieurs niveaux trophiques. Ce projet de la baie d'Hudson aspire à utiliser une approche multifactorielle qui prend en compte des indicateurs à différents niveaux d'organisation biologique afin d'explorer des questions écophysiologiques en lien avec la conservation (McKenzie et al. 2016). Étudier plusieurs niveaux d'organisation nous permet de mieux comprendre non seulement l'effet de la température sur un organisme, mais aussi d'avoir une meilleure idée du mécanisme par lequel les stresseurs agissent. Bien que le projet dans son ensemble ait identifié quatre niveaux d'organisation pour étudier les effets des stresseurs environnementaux (moléculaire,

métabolomique, organisme et écosystémique), mon projet se concentre spécifiquement sur l'effet de la température au niveau de l'organisme entier pour *M. truncata*.

Pour étudier l'effet de la température au niveau de l'organisme entier pour *M. truncata*, j'ai évalué quatre taux physiologiques : la filtration de nourriture, la consommation d'oxygène, l'excrétion d'ammonium et la calcification, à plusieurs températures pour déterminer la capacité métabolique de cette espèce sur un gradient de températures pertinente dans l'écologie de *M. truncata*. Ces informations acquises de manière expérimentale pourront informer des modèles servant à prédire le futur de l'espèce dans un contexte de réchauffement. Dans l'estuaire du Saint-Laurent, d'où proviennent les myes pour cette étude, les températures du fond sur les côtes peuvent atteindre un maximum de 15-16 °C en été (C. McKindsey, communication personnelle). J'émets donc l'hypothèse que les différents taux métaboliques augmenteront avec la température jusqu'à un maximum un peu plus élevé que celle de son environnement naturel, soit autour de 16-17 °C, et suivra une courbe similaire à celle décrite par Fry. Je prédis que la forme des courbes pour les différents taux physiologiques sera différente avec des sensibilités thermiques différentes, ce qui reflète différents mécanismes métaboliques qui sous-tendent des différentes fonctions physiologiques.

CHAPITRE 2
THE EFFECT OF TEMPERATURE ON THE PHYSIOLOGICAL RATES OF *MYA TRUNCATA*

2.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

L'Arctique canadien subit des grandes transformations dues aux changements climatiques, notamment un réchauffement jusqu'à deux fois plus rapide et important qu'observé ailleurs sur la planète. Cela entraine une réduction de la formation de glace qui risque d'avoir un impact sur le fonctionnement des écosystèmes dont les compartiments benthiques et pélagiques sont fortement liés. La mye tronquée, *Mya truncata*, apporte une très grande contribution à la structure de plusieurs écosystèmes arctiques où elle est trouvée en grande densité. Cette espèce de bivalve vivant dans les substrats meubles, crée un lien direct entre la production primaire de surface comme suspensivore et les mammifères marins dont elle est la proie, renforçant le couplage bentho-pélagique dans ces environnements. Jusqu'à maintenant, le manque flagrant d'information sur l'impact de la température sur cette espèce rendait difficile les prédictions quant à son devenir dans un contexte de réchauffement rapide de l'Arctique. L'objectif de ce projet est d'évaluer l'impact de la température sur les taux physiologiques de la mye tronquée pour mieux comprendre les effets possibles du réchauffement sur cette espèce. Le taux de filtration, la consommation d'oxygène, l'excrétion d'ammonium et la calcification ont été mesurés à cinq températures retrouvées actuellement et dans le futur dans l'habitat de la mye (5, 7, 11, 14, 17 °C). Seule la consommation d'oxygène a montré une tendance d'augmentation avec une augmentation de température. Les autres taux n'ont pas été influencés par l'augmentation de la température. La population provenant de l'estuaire du Saint-Laurent, qui se situe vers le sud de l'aire de répartition de cette espèce, semble s'approcher de sa limite thermique à 17 °C. Ces informations nous permettent donc une meilleure compréhension de la physiologie de la mye tronquée afin de

nous éclairer sur les conséquences potentielles du réchauffement global sur cette espèce ainsi que son rôle dans les écosystèmes arctiques.

Mots clés : Changement climatique, Écophysiologie, Tolérance thermique

2.2 ABSTRACT

The Canadian Arctic is currently experiencing major transformations due to climate change, notably, amplified warming that is up to two times the temperature increase observed globally. This warming leads to decreased ice cover, which may impact the functioning of ecosystems for which the benthic and pelagic compartments are tightly linked. The truncate soft-shell clam, *Mya truncata*, provides an important contribution to the structure of many Arctic ecosystems. As a filter feeder, this species which lives in loose sediment, creates a direct link between primary producers and marine mammals and can be found at high densities in certain Arctic regions. Until now, the glaring lack of information on the impact of temperature on this species makes it difficult to predict its future in the rapidly warming Arctic. The objective of this project is to evaluate the impact of temperature on different physiological rates of *M. truncata* to further our understanding of the potential effects of warming on this species. Filtration, oxygen consumption, ammonium excretion and calcification rates were measured at five temperatures found in the clam's current and future habitats (5, 7, 11, 14, 17 °C). Only oxygen consumption showed an increasing trend with increasing temperature. The other rates were not influenced by temperature. The Saint Lawrence Estuary population, near the southern edge of this species' distribution, seemed to approach its upper thermal limit at 17 °C. This information allows us to better understand the physiology of *M. truncata* and enlightens us on the potential consequences global warming could have on this species as well as its role in Arctic ecosystems.

Keywords: Climate change, Ecophysiology, Thermal tolerance

2.3 INTRODUCTION

Many ocean inhabitants are ectotherms, whose metabolism and other physiological functions are directly influenced by the ambient temperature (Fry 1971; Sokolova and Lannig 2008). The Fry Paradigm (Fry 1971) is a conceptual model that describes how environmental factors influence the aerobic scope of an organism which can be defined as the difference between the maximal metabolic rate (i.e., the highest metabolic functioning that an organism can support) and the standard metabolic rate (i.e., the energy required for basic maintenance required for survival at a given temperature). Aerobic scope is a proxy for the energy available for use for activities other than maintenance. As the temperature increases, the standard metabolic rate increases due to the direct effect of heat on metabolic enzymes, while the maximal metabolic rate increases until it reaches a plateau at the upper limit of an organism's metabolic capacity (Fry 1971). This results in the aerobic scope increasing with temperature until a maximum and then decreasing as the standard metabolic rate requires the entirety of the metabolic capacity, resulting in a bell-shaped thermal tolerance curve (Fry 1971). A similar relationship applies to the routine metabolic rate (RMR) – the metabolic rate of organisms undergoing normal behaviours such as digestion and some amount of activity. Pörtner (2001) proposed the oxygen- and capacity- limited thermal tolerance (OCLTT) hypothesis, which states that thermal tolerance as described by the Fry Paradigm, is based on the ability of an organism to supply oxygen to its tissues. At lower temperatures, organisms have an impaired capacity to use oxygen whereas, at higher temperatures, the cardiorespiratory system cannot supply oxygen at the efficiency required to maintain higher metabolic rates (Pörtner 2001, Pörtner et al. 2017).

Both Fry and OCLTT theories are increasingly debated within the community of thermal biologists and may not be applicable to all species (Schulte 2015, Jutfelt et al. 2018). The OCLTT hypothesis and the Fry Paradigm assume that performance and fitness are directly related to aerobic scope and that an organism's thermal optimum for fitness is when its aerobic scope is the greatest. In contrast, studies have reported that optimal growth and reproduction do not correspond to the thermal optimum of the aerobic scope, suggesting that

different physiological functions have different optimal temperatures (Clark et al. 2013, Schulte 2015). In addition, the bell-shaped curve of thermal performance curves suggested by the OCLTT may not be universal (Clark et al. 2013). For example, Munday et al. (2009), demonstrated that the aerobic scope of two coral reef fishes, *Ostorhinchus doederleini* and *O. cyanosoma*, remained high (>70% of maximum) until very near their lethal limit, suggesting that oxygen limitation may only appear at or very near lethal limits. Despite the debate and uncertainties surrounding mechanisms, the geographic distribution of ectotherms is heavily influenced by an organism's thermal tolerance and thus why thermal thresholds can be used as indicators for environmental stressors (Pörtner 2001, McKenzie et al. 2016). Because many population dynamic features can be attributed to the effects of environmental stress on individuals, an imbalance of energy expenditure may lead to a decline in overall population growth (Beukema et al. 2009, Thomas and Bacher 2018).

A growing focus in ecophysiology and ecology is the use of models to predict the effect of environmental changes on organisms and their distribution (McKenzie et al. 2016). Temperature sensitivity and limits data are a crucial aspect for developing and implementing these models. One such model, the Dynamic Energy Budget (DEB) model, uses the Arrhenius temperature (T_A; see overview in Carvalho-Silva et al. 2019) to incorporate temperature effects on physiological rates (Kooijman 2000). This model assumes that T_A is constant across all physiological rates (Koojiman 2000), although there is evidence that while most physiological rates tend to vary positively with temperature, they may display different response curves. The shape of a thermal performance curve depends on the underlying biochemical processes that control a given rate, potentially leading to a variety of thermal performance curves at the whole-organism level (Schulte et al. 2011). For instance, several bivalves, some of the most studied marine ectotherms, demonstrate varying response rates to temperature. For the oyster *Ostrea edulis*, maximum clearance rates were observed at 15 °C, whereas oxygen consumption was consistent between 5 °C to 20 °C with a rapid increase at 25 °C (Buxton et al. 1981). The mussel *Modiolus barbatus* exhibited increasing clearance rates with increasing temperature (9-28 °C), but oxygen consumption was highest at the lowest temperature tested (Ezgeta-Balić et al. 2011). Experimentally derived information on

thermal tolerance and limits could inform models to predict the future of a species in the context of warming waters (Teal et al. 2018). This is especially important in areas experiencing major and rapid transformations due to the consequences of climate change such as the Canadian Arctic.

In this area, decreasing sea ice cover during the year allows the ocean to absorb more radiation, leading to amplified warming, up to two times the temperature increase observed globally (Stewart and Lockhart 2005, Hamilton 2013). Arctic and subarctic ecosystems have tight benthic-pelagic coupling which provides stability and resilience (Grebmeier et al. 2006, Hoover et al. 2013a, McMeans et al. 2013). However, global change may disrupt this coupling and thus ecosystem stability through reduced ice cover, altering the input of carbon supply to the benthos and shifting the energy flow to favour pelagic production (Grebmeier et al. 2006, Wesławski et al. 2011; McMeans et al. 2013). Filter-feeding bivalves play a crucial role in maintaining benthic-pelagic coupling by filtering the water column, concentrating organic matter in the benthos through depositing digested and undigested remains, and making it available for other benthic organisms, and as prey to higher level predators (Welch et al. 1992, Newell 2004).

An important suspension feeder in Arctic benthic ecosystems is the truncate soft-shell clam, *Mya truncata* (L. 1758), a slow-growing, long-lived (up to 62 years) species (Welch et al. 1992, Siferd 2005). The species has a boreal-arctic distribution in shallow waters to 80 m depth and can reach densities of 136 individuals per m^2 in certain Arctic regions (Welch et al. 1992; Amaro et al. 2003). Its range extends south to Massachusetts Bay, Massachusetts, U.S.A. (Lubinsky 1980). Due to their high density, *M. truncata* may contribute significantly to benthic-pelagic coupling across the Arctic. At its highest densities in Lancaster Sound, *M. truncata* can filter the equivalent of the whole 0 to 15 m water column in two to three weeks, providing an important source of nutrients for deposit feeders by releasing undigested pseudofeces to the seafloor (Welch et al. 1992). *Mya truncata*, like many other invertebrates, provides a critical link between primary producers and higher trophic levels as it is preyed upon by walruses (*Odobenus rosmarus*) and bearded seals (*Erignathus barbatus*),

transferring energy to upper trophic levels and leaving unconsumed biomass for scavengers and decomposers (Welch and Martin-Bergmann 1990, Hobson and Welch 1992). The species also has cultural importance for many Inuit communities as a subsistence food source, which plays a crucial role in food security (NCRI 2008, Wenzel 2009). Rapinski et al. (2018) argues that the harvest of seashore organisms, such as *M. truncata,* is likely to increase as changing environmental conditions, such as unstable ice, makes hunting and fishing less reliable.

Despite the important ecological and cultural role that *M. truncata* play in the Arctic, knowledge of its ecophysiology, specifically related to its response to temperature, is lacking. *M. truncata*'s long lifespan and sedentary nature makes it slow to respond to new environmental conditions and could make it vulnerable to warming. Although there is evidence that temperature may affect *M. truncata* distribution, no experimental data are available on thermal tolerances and limits for this species (Amaro et al. 2005, Sleight et al. 2018). *Mya truncata* have been found from sub-zero temperatures in Arctic regions up to 15 °C in Scotland and the White Sea (Hewitt and Dale 1984, Günther and Fedyakov 2000, Sleight et al. 2018). A one-degree increase from 15 to 16 °C under laboratory conditions resulted in less shell repair and an up-regulation of stress response genes (Sleight et al. 2018). A limited physiological knowledge base is a major constraint for management and conservation (McKenzie et al. 2016). The present study addresses knowledge gaps on the effect of temperature on *M. truncata* physiological rates to better understand the pressures that global warming may pose for this key circumpolar species. We evaluated four rates: filtration, oxygen consumption, ammonium excretion, and calcification, at various temperatures to determine the metabolic capacity of this species under an ecologically relevant range of temperatures. We hypothesized that physiological rates increase with temperature until reaching a maximum, which we anticipate will occur at a slightly higher temperature (i.e., 16 °C) than the ones at which *M. truncata* has typically been exposed to in its natural environment, with a curve similar to that described by Fry and OCLTT, although different rates may display different thermal responses due to underlying mechanisms. We also calculated the Arrhenius temperature for oxygen consumption to determine the thermal

sensitivity of *M. truncata* and help to understand the sensitivity of this species to changing temperatures.

2.4 METHODS AND MATERIALS

2.4.1 Husbandry

Four hundred and thirty adult *Mya truncata* were collected in October 2020 from Godbout, QC, (49.3206, -67.58898) by SCUBA divers at about 10 m depth when the water temperature was ~ -1 °C and salinity of ~ 28. Clams were transported to the Maurice Lamontagne Institute (MLI) within 24 h following capture in coolers between sheets of wet cloth to reduce shock and desiccation stress. Upon arrival, clams were patted dry and marked with 3 mm beekeeper numbers (Propolis-etc, St-Mathieu de Beloeil, Canada) that were attached using gorilla glue on the left valve and left to dry for ~5 min before placing them back in water. During this time, clams were measured for shell length, height, and width with digital calipers to a precision of 0.01 mm. Clams with cracked or otherwise damaged shells were not used for the experiments. Initially, clams were held in a large holding system for acclimation (five months). The system consisted of four, 500 L tanks, within which the clams were randomly distributed and supplied with recirculated water (12 L min^{-1}) from a 500 L header tank. The water in the header tank was filtered mechanically using a sand filter (VARI FLO XL, Hayward Industries Inc, MD, USA), and maintained at 5 °C with a 2 hp chiller. Water in the header tank was replenished continuously with fresh sea water (12 L min^{-1}) sourced directly from the Saint Lawrence Estuary (48º 39' 31.752"N, 68º 09' 24.151"W). Salinity was maintained at 28, as determined by the salinity intake water. A layer of sand (15 cm deep, washed, fine grade) was added to each tank, within which the clams were buried manually at a depth at which only their siphons were visible above the substrate, in an attempt to recreate their habitat to achieve an ecological realism. Clams were fed every day at approximately 11 am with a concentration of ~0.05 mL L^{-1} of Shellfish diet 1800 composed of five marine algae, *Isochrysis* sp., *Pavlova* sp., *Tetraselmis* sp., *Thalassiosira weissflogii*, and *Thalassiosira pseudonana* (Reed Mariculture Inc., CA, USA). To prevent the food from

draining, water inflow to the tanks was halted for 1 h after adding the algae. Temperature, pH, salinity, and dissolved oxygen were monitored daily with a multiparameter Waterproof meter (HI9829, Hanna Instruments Inc., RI, USA). The sand filter was backwashed once a week, and clam mortality checked daily. Clams whose siphons showed signs of white around them and/or no reaction to a mechanical stimulus were considered dead and removed. The tanks were illuminated with red strip lights, with the photoperiod in the room set to mimic the photoperiod in Mont-Joli, QC. In May, the photoperiod was approximately 5 am to 8 pm but varied depending on the daily light patterns. After five months, 300 clams were dug up and transferred into the experimental system.

2.4.2 Experimental system and setup

Temperatures used in the experiments were 5, 7, 11, 14, 17 °C. They were chosen to cover the temperature range experienced by *M. truncata* in their natural setting while avoiding high mortality at higher temperatures. Temperature data from the Saint Lawrence Estuary indicate that the bottom temperatures along the coast where high densities of *M. truncata* are found reach a maximum of 15-16 ˚C in the summer (C. McKindsey, personal communication). Preliminary temperature experiments showed high mortality rates at 19 °C for *M. truncata* and a previous study on thermal stress in *M. truncata* determined that there were signs of stress at 16 ˚C, only one degree above the temperature maximum in the region (Sleight et al. 2018)

Upon transfer from the holding tanks to the experimental system, length measurements were taken once again. The experimental system (Fig 2) was designed to be portable to allow for it to be transported to remote locations to facilitate on-site laboratory tests in northern communities with minimal infrastructure in place for such studies. This system consisted of three insulated and collapsible raceways (2000 L), each equipped with a chiller (Delta Star DS-6, 1/2 hp, Aqua Logic Inc, NC, USA), and ten 15 L experimental tanks, two per temperature treatment per raceway. The experimental tanks were housed in the raceways (used as water baths) but held up with plastic platforms so that the water in the tanks did not

mix with the water from the raceway. Environmental conditions and water flow were monitored and controlled by an aquarium controller system (A3 Apex System, Neptune Systems, Morgan Hill, CA, USA). These consisted of dosing meters to regulate flow to tanks, and temperature and pH probes to provide remote access and real-time notifications through the cloud-based Apex Fusion application. A header tank of water sourced from the Saint Lawrence Estuary fed into each experimental tank using dosing meters from the Apex system set at ~120 L d^{-1}. The temperature of the experimental tanks was controlled by the cold inflow originating from the header tank and individual heaters (100 W TH-C 100 titanium aquarium heater, Aquatop, CA, USA, temperature range = 20 °C – 33.3 °C) in each tank that were programmed using Apex system sensors. The water in each tank was kept well oxygenated by continuous air bubbling. Temperature was logged every minute with the Apex Fusion system and manually verified each day with a handheld thermometer (Fluke 52 II dual-input digital thermometer, WA, USA). The dosing lines were looped in the raceway to keep the water coming into the treatment tanks as cold as possible. Tanks for the higher temperature treatments (11, 14, 17 °C) were insulated with foam insulation panels to keep stable temperatures.

Clams were placed in individual pots, either 250 mL glass jars for the larger clams or 100 mL plastic containers for the smaller specimens, filled about three quarters full will sand, which were then placed in the experimental tanks. Clams were randomly placed in one of 30, 15 L-tanks, with 10 individuals per tank. After a two-week habituation period, the temperatures were ramped at a rate of 2 °C d^{-1} starting from 5 °C until the required temperature was reached. Following ramping, clams were held at five different temperature treatments: 5, 7, 11, 14, and 17 °C, for two weeks (see Figure 3 for timeline). Each day at 11 am, Shellfish diet 1800 was added to individual tanks to attain a concentration of 0.05 mL L^{-1} and the water flow was stopped for one hour. Mortality was checked daily during the experiment and individuals with no reaction when the siphon was stimulated were considered dead and removed. Twelve clams of similar size were chosen from each temperature treatment for physiological rate measurements to minimize the effect of size on the results. Because of the ramping procedure, each temperature treatment reached its exposure

temperature at a different time, therefore the rates for each temperature were all taken over the same two days, with rates being measured on the coldest treatment (5 °C) first and the warmest treatment (17 °C) last. Due to a system malfunction in one of the raceways on day 2 of the experimental period, the clams from that raceway were not used for the 11, 14, and 17 °C temperature treatments. Despite this, we were able to keep the sample size constant (n = 12) by sampling clams from the other two raceways.

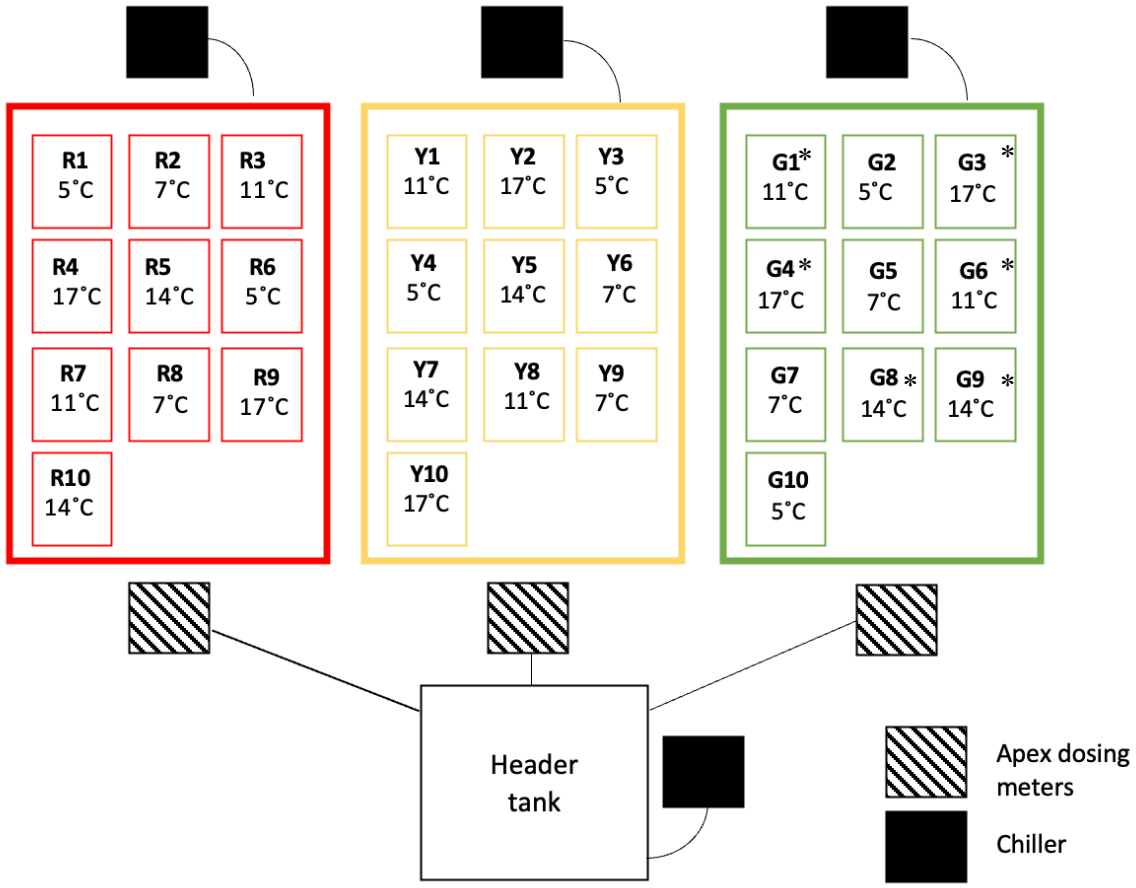


Figure 2. Diagram of the experimental system. Each large, coloured box represents a raceway, and the smaller boxes inside are the individual tanks which were controlled individually with chilled water from the dosing meters going directly from the header tank into each experimental tank and individual heaters in each tank. Asterisks indicate tanks that were not used due to a system malfunction (see section 2.4.2 for further details).

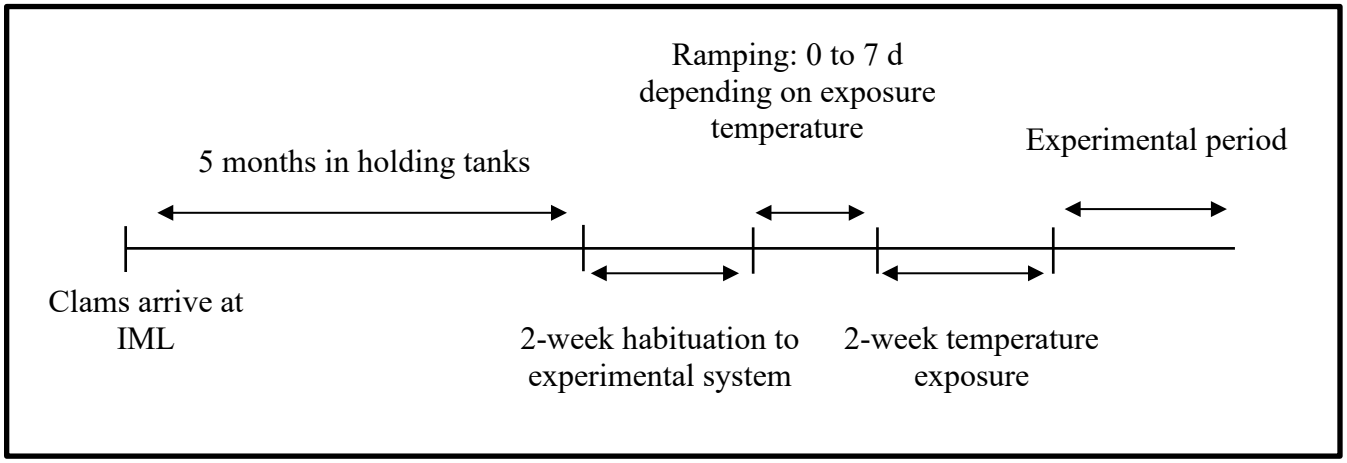


Figure 3. Timeline of experiment. The temperature in the holding tanks and during the habituation period was 5 °C. The ramping rate was 2 °C d^{-1} to exposure temperatures of 5, 7, 11, 14 and 17. The physiological rates for each temperature were all taken over the same two days, filtration rate on the first day and oxygen consumption, ammonium excretion and calcification the second day, with rates being measured on the coldest treatment (5 °C) first and the warmest treatment (17 °C) last.

2.4.3 Determination of rates

2.4.3.1 Filtration

At the end of the 2-week exposure period, clams were fasted for two days before beginning the feeding trials. Glass jars of 1.5 L were filled with 1300 mL of filtered water (three filter line - 5-micron, 1-micron, 0.2-micron, UV sterilized Aqua UV, CA, USA) at the treatment temperature. The jars were placed in the same tanks as where the clams were taken from to ensure that temperatures were maintained and on target. Each jar had an air stone bubbling air to ensure mixing and oxygenation. Clams, still in their individual pots of sand were transferred into the feeding jars and left for one hour before beginning the filtration trail. Then, 200 µL of shellfish diet 1800 mix was added to each jar to reach a concentration of approximately 150 µL L^{-1}. An initial 50 mL sample was taken from each jar and filtered on 25 mm Whatman ® GF/F microfilters with a porosity of 0.7 µm. At the end of a four-hour

period, the same sampling procedure was repeated. All filters were labelled, wrapped in aluminium foil, and stored at –80 °C. A blank (i.e., without a clam in the jar) was run at each temperature following the trial to ensure that the mix concentration remained constant.

To determine the decrease in algae concentration throughout the trials, concentrations of chlorophyll a and phaeopigments were measured by fluorometry (10-AU, Turner design, CA, USA) using the acidification method (Parsons et al. 1984). This process was conducted in a room with only green lights to prevent pigment deterioration. Frozen filters were ground three times for 5 sec each with a sonificator (Q125, QSonica, CT, USA) set to approximately 94 watts and left for 24 h in the dark at 4 °C for extraction using 10 mL of 90% acetone. After 24 h, the absorbance of the 10 mL supernatant was measured, after which the supernatant was acidified with three drops of HCl 5% before taking another reading.

Filtration rates (in mL seawater min^{-1}) were calculated following Eq 1:

$$F = V \times \frac{\ln[C_i] - \ln[C_f]}{\Delta t} \quad [1]$$

where [Ci] and [Cf] (in µg of chlorophyll-a and phaeopigments L^{-1}) were respectively the initial and final cell concentrations is the chamber water; V (in L) is the volume of water in the jar; and Δt (in h) is the incubation time.

2.4.3.2 Oxygen consumption

The respirometry set up (Figure 4) consisted of three 60 L coolers filled with filtered water (three filter line: 5 µm, 1 µm, 0.2 µm, UV sterilized Aqua UV, CA, USA), each with a cooling/heating coil that was connected to a refrigerated circulating bath (VWR Model AD 7L R-20 or VWR MX 7L R-20, PA, USA) to control the temperature in the coolers. Four, 1.2 L respirometers made of mason jars and plastic twist on lids were placed in each cooler

and attached to 12-V DC aquarium pumps set to 1 L min^{-1} by quick-release clips. This ensured a flow-through system that could also be closed to create a recirculation loop ensuring good homogenisation in the closed chamber. An air stone was placed in each cooler to ensure maximal oxygenation when the chambers were open. They were removed when chambers were closed for oxygen consumption trials. The respirometers were wrapped in black electrical tape to limit light disturbance that could influence the oxygen consumption rates.

At the end of the two-week temperature exposure experiments and following the filtration trials (see previous section), the clams were transferred into the respirometers the night before the beginning of the trials for fasting and habituation. A total of ~200 g of flat glass beads (~ 1 cm X 0.5 cm) was placed in each respirometer to serve as support to the clams and reduce the volume of water to amplify changes in oxygen concentration. The clips on the respirometers were open during the night to allow the water to be continually exchanged with water from the coolers. The next morning, 15 L of filtered water at the same temperature was added to the coolers to refresh the water.

Closed respirometry trials were conducted to cover the habitual feeding period from 11 am to 12 pm. The measurement period ranged between 2-5 h with oxygen measurements taken manually every 15-30 minutes, depending on the temperature. Oxygen concentration was logged in % air saturation for each chamber using a single handheld non-invasive fibre optic system for all respirometers (FIBOX 4, PreSens, Regensburg, Germany), which allowed for measurements without opening incubation chambers. The % air saturation never went below 60%.

The % air saturation was converted to oxygen concentration (μmol L^{-1}) by calculating the concentration of 100 % air saturation using the initial temperature, salinity and pressure measurements recorded by the sensor for each clam. The oxygen consumption rate corresponded to the slope of the regression fitted to the oxygen concentration decline over

time and corrected by chamber volume, including the volume of the tubing, and removing the wet mass of the clam including the shell and the beads.

Blanks were conducted for each respirometer following each trial by running a new trial without a clam for approximately 2 h to correct for background oxygen consumption due to bacterial oxygen consumption. Regression slopes generated from the blank trials were subtracted from the slope of the respirometry trial.

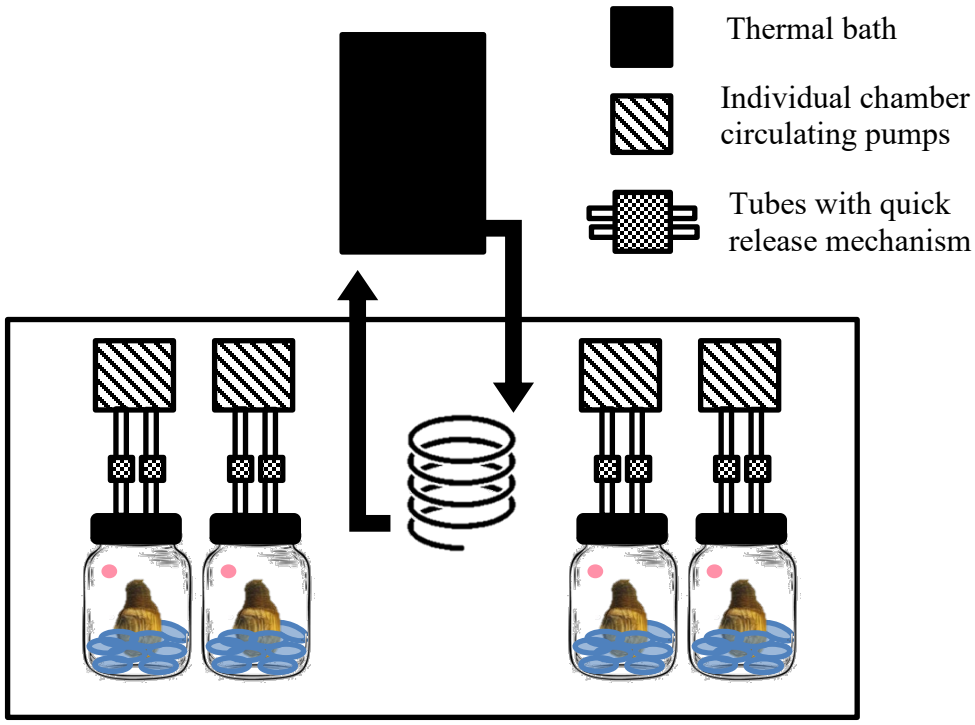


Figure 4. Diagram representing one of the cooler systems used for respirometry trials. A thermal bath regulated the water temperature in the cooler through a heating/cooling coil placed in the cooler. The pink dots are where the sensors read the oxygen levels inside of the jars and the blue circles represent glass beads which hold the clams upright. An air stone was placed in the cooler to provide circulation and a consistent temperature throughout.

2.4.3.3. Ammonium excretion and calcification

At the beginning and end of respirometry trials, seawater was sampled for ammonium concentration and total alkalinity. Samples of 100 mL of sea water were taken for each variable directly from the cooler at the beginning of the respirometry trial and from each respirometer at the end. Thirty mL samples were used for ammonium concentrations by filtering through inline GF/F 0.7 µm filters into 100 mL borosilicate glass bottles and fixed with 1mL of nitroprussiate phenol solution and 1mL of chlorine complexent alkaline solution.

Ammonium concentrations were determined using the Solorzano method (Solorzano 1969) based on spectrophotometry at a wavelength of 630 nm. A calibration curve was prepared with ammonium sulfate before the analysis, treating them the same way as the samples to determine the concentration of ammonium in each sample.

Excretion rates (in µmol h^{-1}) were calculated as follows:

$$E = \frac{\Delta NH_4^+ \times V}{\Delta t} \quad [2]$$

where ΔNH_4^+ (µmol NH_4^+ L^{-1}) is the difference between initial and final NH_4^+ concentrations; V (in L) is the volume of the chamber and tubing minus *M. truncata* wet weight as an approximation of volume and the volume of the glass beads; Δt (in h) is the incubation time.

Water samples of 100 mL were taken for alkalinity and filtered on 0.7 µM GF/F filters into 100 mL borosilicate glass bottles and fixed with a drop of mercuric chloride to stop any biological activity. All samples were stored in the dark at room temperature before analysis.

Net calcification was estimated using the alkalinity anomaly technique (Smith and Key 1975). Total alkalinity (A_T) of each sample was measured by 0.01 N HCl titration on an automatic titrator (848 Titrino plus, Metrom, FL, USA) and using the Gran method (non-linear least-squares fit) applied to pH values from 3.5 to 3.0 (Dickson et al. 2007). For each

mole of $CaCO_3$ precipitated, A_T decreases by two equivalents, while ammonium production increases A_T in a mole-to-mole ratio (Wolf-Gladrow et al. 2007). Net calcification is thus calculated by correcting the alkalinity variation by ammonium flux such as:

$$G_n = \frac{-(\Delta A_T - \Delta \mathrm{NH}_4^+) \times V}{2 \times \Delta t} \quad [3]$$

where ΔA_T is the difference between initial and final total alkalinity concentrations (μ Eq L^{-1}); $\Delta \mathrm{NH}_4^+$ (μmol NH_4^+ L^{-1}) is the difference between initial and final NH_4^+ concentrations; V (in L) is the volume of the chamber minus *M. truncata* wet mass and the beads; and Δt (in h) is the incubation time.

The top two temperature treatments (14 and 17 °C) were discarded for both ammonium excretion and calcification because a different reagent than the one that was employed at lower temperatures was used, which led to inconsistent results.

2.4.4 Arrhenius temperature

The Arrhenius temperature (T_A) was calculated for each rate by plotting natural logarithm of each rate over temperature (in K). The slope of the resulting linear relationship ($-T_A$) can be used to describe the dependence of a rate on temperature (Kooijman 2000). To see the effects of extreme temperatures, calculations were done for three different scenarios: all the values, excluding the top temperature, and excluding the top two temperatures.

2.4.5 Statistical analyses

Statistical tests were used to evaluate if the various quantified rates varied with respect to temperature. First, a Pearson correlation test was run on each rate *versus* clam dry weight to ensure the absence of body size influence. Then, random effects from spatial pseudo

replication (i.e., tanks and raceways, Figure 1) were evaluated using linear mixed effect models and not included in analyses when not significant. Normality and homogeneity of variance were checked using Shapiro-Wilks test and Levene's test, respectively, prior to statistical analyses. Because no physiological rates met assumptions, and no random effect was significant, all data were analysed using non-parametric Kruskal-Wallis tests. A Dunn post hoc test with a Bonferroni adjustment was applied to identify differences between temperatures when the Kruskal-Wallis test showed significant results. A Pearson correlation test was used to determine the relationships between each of the rates. The coefficient of variance was calculated at each temperature treatment for all rates except for calcification because this method does not accurately represent the variability when values are negative and positive. A mean Whitney Wilcox test was used to compare calcification rate to 0, to determine if there was a rate measured. All statistical analyses were performed using RStudio (version 1.4.1717; R Core Team 2023; packs: dunn.test, car, lmer, lmerTest, ggpubr) with an alpha = 0.05.

2.5 RESULTS

2.5.1 Experimental conditions during exposure (water quality and clam conditions)

Temperature was stable during the exposure period with a variability less than ±1 °C for each treatment while all other water quality metrics remained stable and similar across treatments (Table 1). Dry body mass of clams did not differ significantly among temperature treatments ($F = 1.27$, $df = 4$, $p = 0.294$). Mortality was low in all treatments with a maximum of four individuals dying at the 11 °C treatment over the two-week exposure period (Table 1). However, clams at 17 °C had hyperextended and soft siphons and responded slowly to stimuli.

Table 1. Summary of mean (± SD) seawater parameters, size of *Mya truncata* including the dry weight (DW) of the body mass without the shell and shell length, and mortality for each temperature treatment during the two-week temperature exposure period. Twelve clams were sampled for size measurements. Water parameters were taken from 6 tanks per temperature for 5 and 7 °C temperatures and from 4 tanks for 11, 14, 17 °C because of a raceway malfunction. Sea water parameters measurements were taken daily over the two-week exposure period.

Temperature (°C)	Mortality (individuals)	Weight (g DW)	Shell Length (mm)	pH	Salinity (PSU)	Dissolved Oxygen (%)
5.0 ± 0.4	0	4.00 ± 0.61	58.99 ± 2.16	7.89 ± 0.12	26.61 ± 1.23	99.9 ± 3.2
6.9 ± 0.3	0	3.43 ± 0.64	57.25 ± 3.79	7.86 ± 0.05	27.29 ± 0.78	98.2 ± 2.4
11.2 ± 0.5	4	3.74 ± 0.56	58.36 ±3.53	7.81 ± 0.04	27.5 ± 0.43	96.7 ± 3.3
13.9 ± 0.7	0	3.68 ± 0.72	58.36 ± 4.13	7.83 ± 0.04	27.39 ± 0.58	94.4 ± 3.0
16.3 ± 0.4	3	3.60 ± 0.58	58.64 ± 5.04	7.80 ± 0.08	27.43 ± 0.49	94.9 ± 4.3

2.5.2 Physiological Rates

There were no significant correlations between dry body mass and any of the measured physiological rates with all temperatures combined for the same rate (p-value <0.05 and R < 0.3 for all correlations). Rates were thus not reported as mass-specific values.

Table 2. The coefficient of variation (%) for filtration rate, oxygen consumption rate and ammonium excretion rate for the temperatures measured. Coefficient of variation calculated as SD divided by the mean times 100.

	Coefficient of variation %		
Temperature (°C)	Filtration rate	Oxygen consumption rate	Ammonium excretion rate
5	89.7	49.1	50.0
7	55.8	44.7	84.6
11	69.5	53.8	81.1
14	53.7	51.3	NA
17	50.8	68.7	NA

2.5.3 Filtration

Filtration rate did not vary with respect to temperature (Kruskal Wallis test, chi-squared = 3.485, df = 4, p = 0.480). Values ranged between 0 mL min^{-1} and 5.63 mL min^{-1} with an average value of 1.67 mL min^{-1} ± 0.14 SE for all pooled temperatures (Fig 5). The coefficient of variation ranged between 50.81% at 14 °C and 89.71% at 7 °C (Table 2). Filtration rate was not correlated with any other rates ($p > 0.05$).

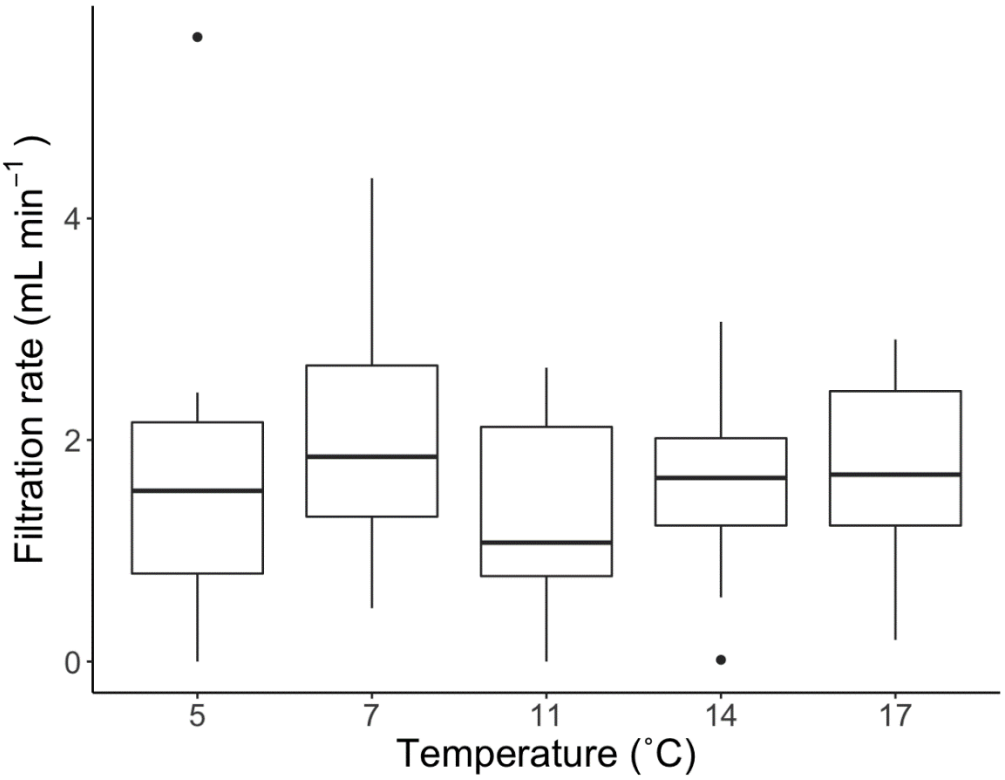


Figure 5. Filtration rates in mL min^{-1} indiv^{-1} at five temperatures for *Mya truncata*, n=12 individuals per temperature. Boxplots represent the interquartile range with the lower limit being the first quartile, the line in the middle is the median, and the upper limit of the box is the third quartile. The whiskers represent scores outside of the middle 50%.

2.5.4 Oxygen consumption

Oxygen consumption increased significantly with the increase of temperature (Fig 6; Kruskal Wallis test, chi-squared = 9.963, df = 4, p value = 0.04). However, the post hoc Dunn test did not determine which treatments differed, likely due to the very conservative Bonferroni correction. In general, the oxygen consumption data showed increasing variability as temperature increased. The four lower temperatures had coefficients of variation ranging from 44.7 to 53.78% whereas it was 68.71% at 17 °C. There is a strong correlation between oxygen consumption and excretion rates (Fig 7).

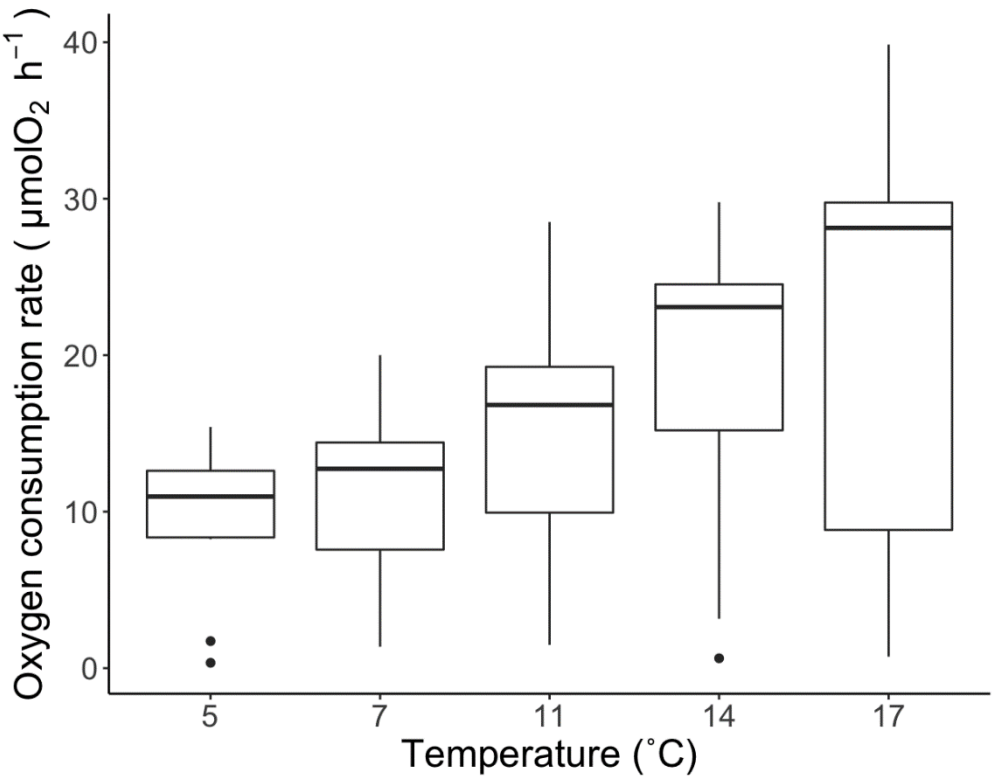


Figure 6. Oxygen consumption rates in µmol O_2 h^{-1} $indiv^{-1}$ at five temperatures for *M. truncata*, n=12 individuals per temperature.

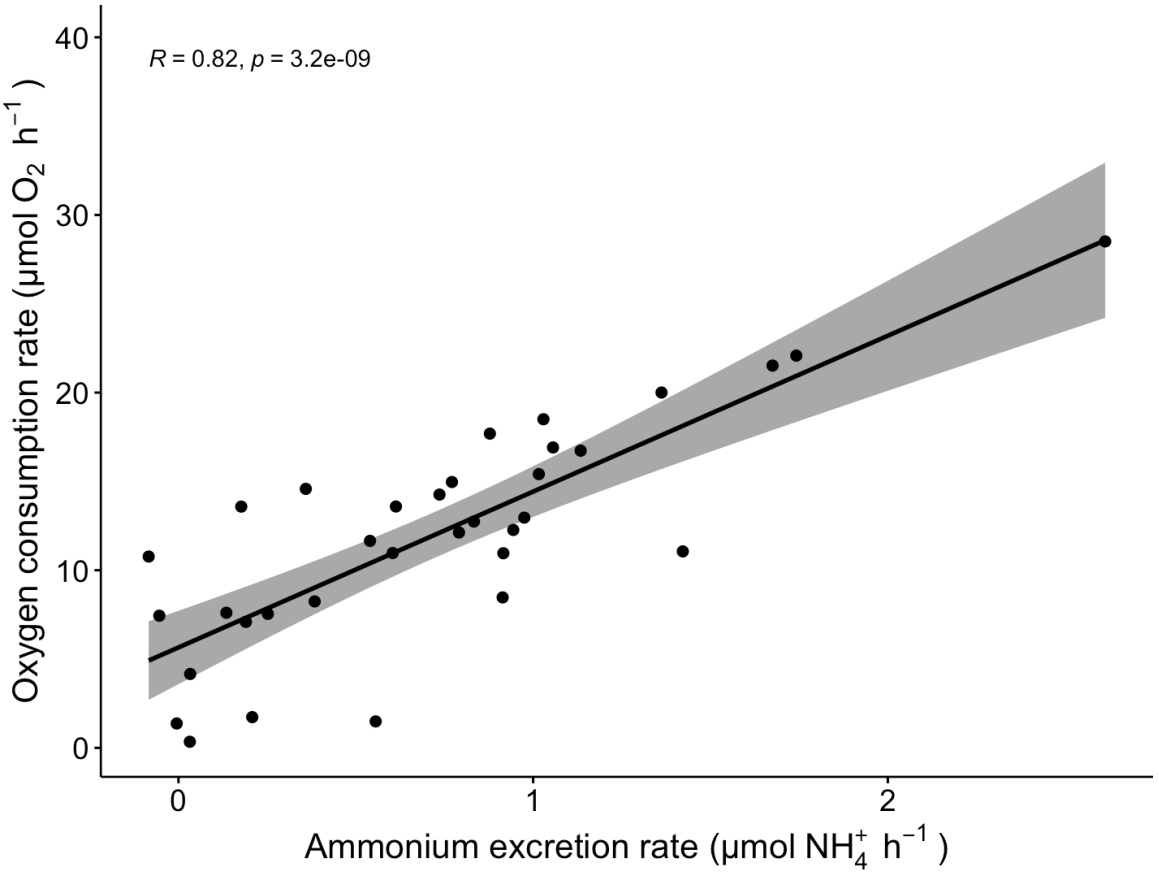


Figure 7. Pearson correlation between ammonium excretion rates (µmol NH_4^+ h^{-1}) and oxygen consumptions rates (µmol O_2 h^{-1}) for *M. truncata*.

2.5.5 Excretion

Values ranged between 0.054 µmol NH_4^+ h^{-1} and 1.742 µmol NH_4^+ h^{-1} with an average value of 0.714 µmol NH_4^+ h^{-1} ± 0.070 SE for all pooled temperatures. Mean ammonium excretion rates did not vary significantly among the three coldest experimental temperature treatments (Fig 8; Kruskal Wallis test, chi-square = 4.504, df = 2, p = 0.105). The coefficient of variation ranged from 50.04 % at 5 °C to 84.60 % at 11 °C. Excretion rate was correlated with only oxygen consumption rate (Fig 7).

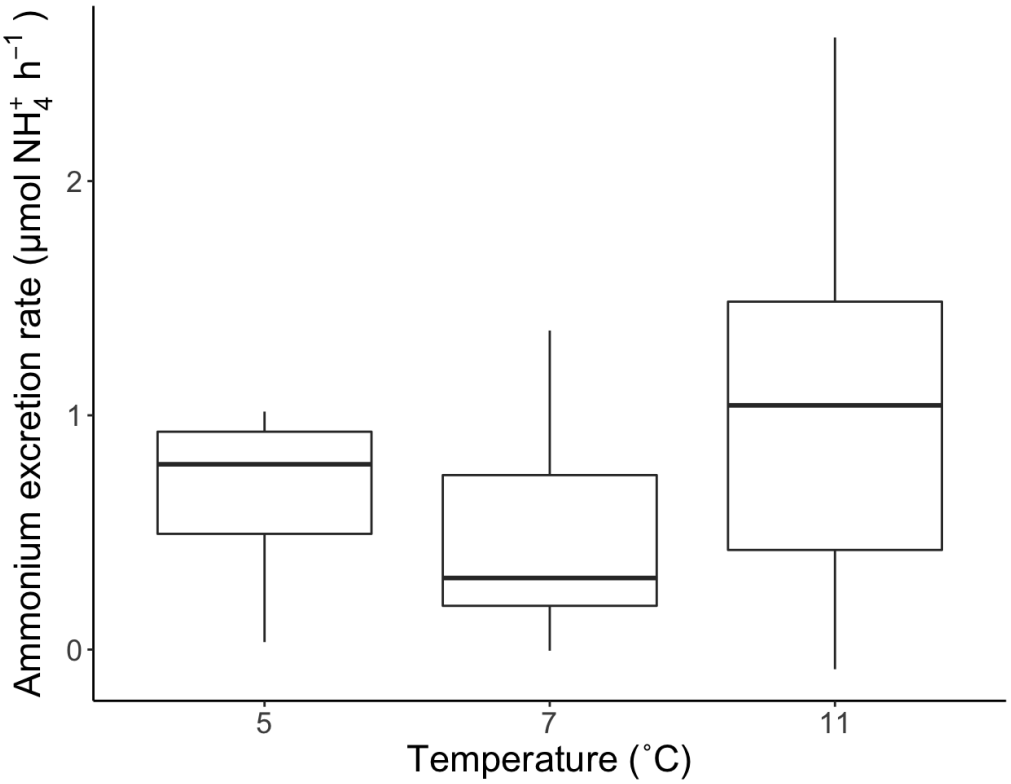


Figure 8. Ammonium excretion rates in µmol NH_4^+ h^{-1} $indiv^{-1}$ at three temperatures for *M. truncata* n=12 individuals per temperature.

2.5.6 Calcification

Calcification rate did not vary significantly with respect to temperature (Fig 9; chi-square = 0.796, df = 2, p = 0.673). Values ranged between -18.88 µmol $CaCO_2$ h^{-1} and 21.09 µmol $CaCO_2$ h^{-1} with a pooled average of 0.94 ± 0.92 SD µmol $CaCO_2$ h^{-1}. While no variation due to temperature was measured, the rates measured were not equal to 0 (V= 1649.5, p-value = 8.0e-10). Calcification rate was not correlated with any other rates (p > 0.05).

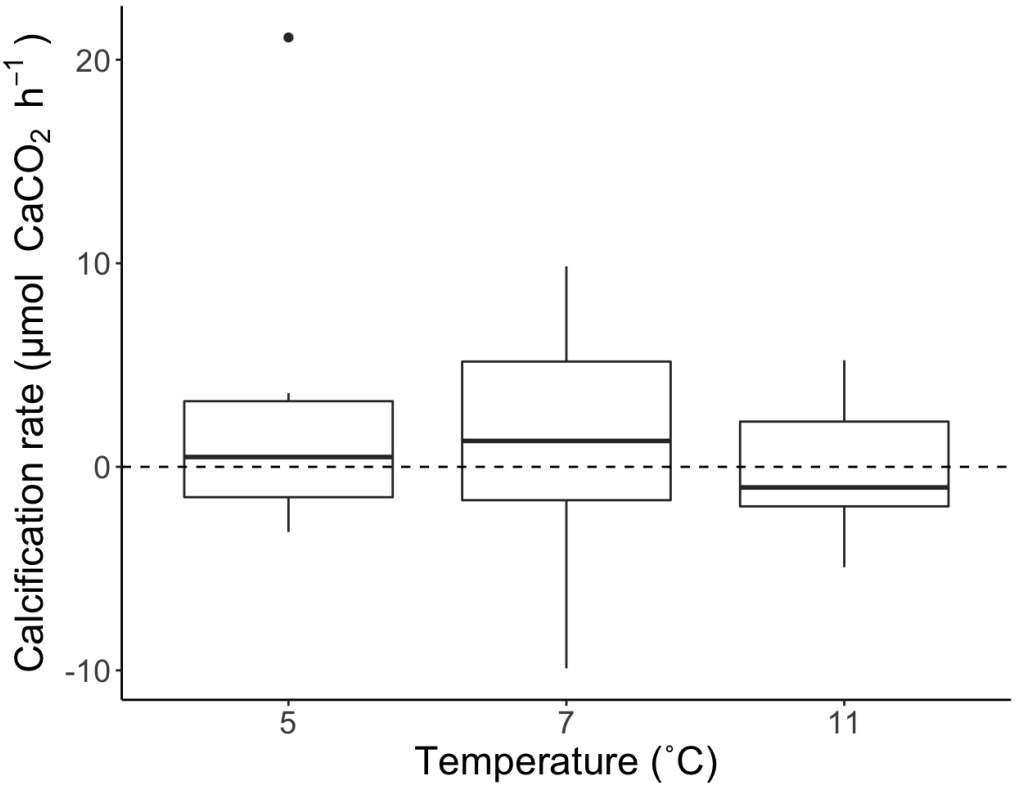


Figure 9. Individual calcification rates (µmol $CaCO_2$ h^{-1}) at three temperatures for *M. truncata* n=12 individuals per temperature. Values below the dashed line indicate shell dissolution while those above the line indicate calcification.

2.5.7. Arrhenius temperature

Because the oxygen consumption rate showed the clearest trend with temperature and had data for all the five temperature treatments, the Arrhenius temperature (T_A) was calculated with all the points, resulting in a T_A of 3598. However, T_A represents the rate of increase with temperature on the linear part of the thermal performance curve. Because of high inter-individual variability, the confidence intervals for the slopes were all very high and intersected with each other, suggesting that there was no statistical difference (Fig 10). T_A for all calculations along with comparative values from the literature can be found in Table 3.

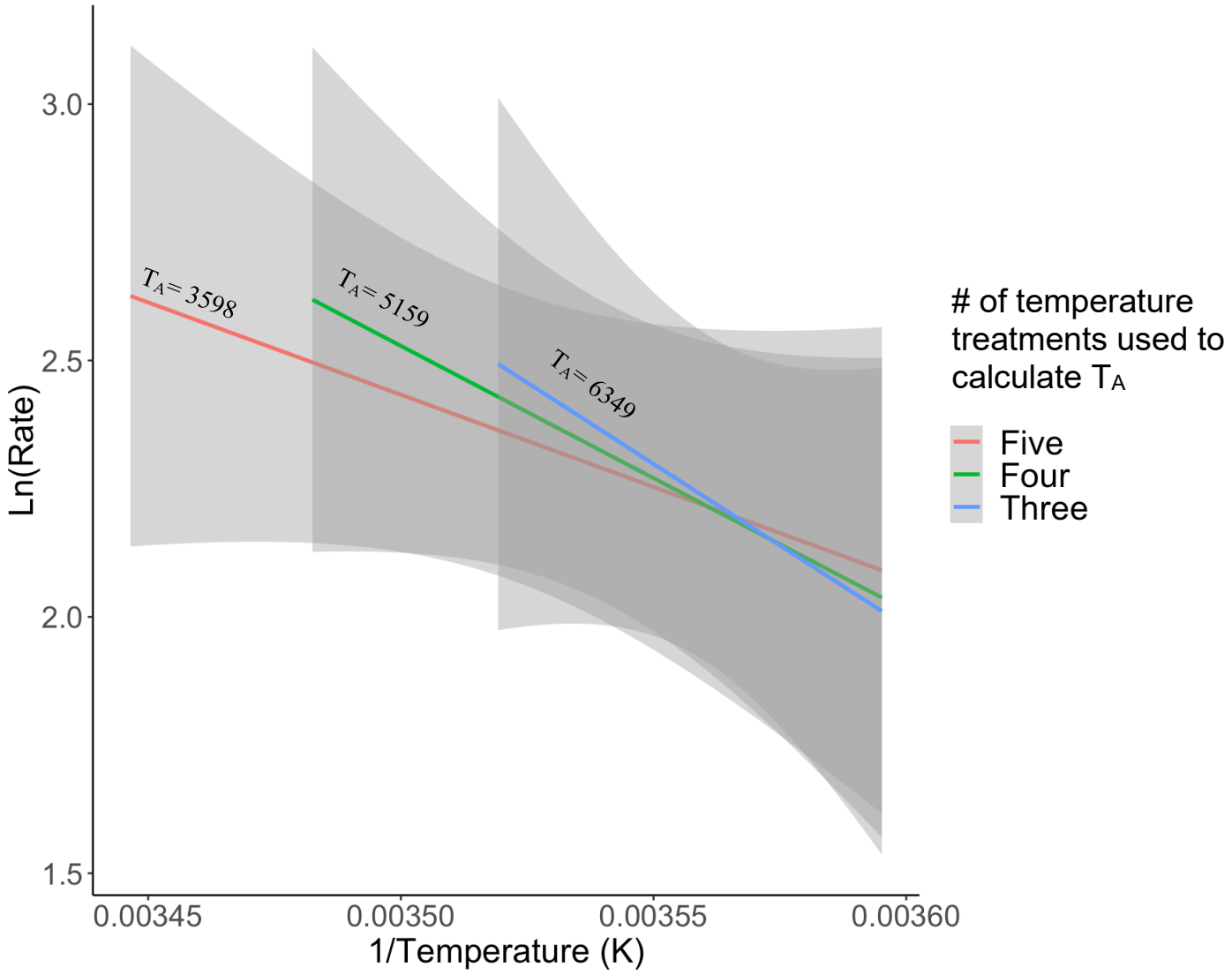


Figure 10. The Arrhenius temperature (T_A) for *Mya truncata* using oxygen consumption data for all the temperature treatments (Five), excluding the top temperature treatment (Four) and excluding the top two temperature treatments (Three). T_A is calculated as the slope of the natural logarithm of the rate over the inverse temperature in K.

Table 3. Comparative table for Arrhenius temperatures for bivalves. The distribution for *Perna perna* and *Mytilus galloprovincialis* is representative of where the samples for that study were taken because it was investigating an environmental gradient. References in parentheses indicate the original source of the data used to calculate the Arrhenius temperature, while the "Reference" column is the article that calculated the Arrhenius temperature.

Species	Arrhenius temperature	Region/habitat	Rate used	Reference
Mya truncata	3598	Arctic/intertidal to subtidal	Oxygen consumption 5, 7, 11, 14, 17 ˚C	This study
Mya truncata	5159	Arctic/intertidal to subtidal	Oxygen consumption 5, 7, 11, 14 ˚C	This study
Mya truncata	6349	Arctic/intertidal to subtidal	Oxygen consumption 5, 7, 11 ˚C	This study
Macoma balthica	5672 ± 522	Temperate/upper intertidal	Oxygen consumption (De Wilde 1975, Wilson and Elkaim 1991)	van der Veer et al. 2006
Mya arenaria	7051 ± 453	Temperate/intertidal	Oxygen consumption (Kennedy and Mihursky 1972, Lewis and Cerrato 1997)	van der Veer et al. 2006
Cerastoderma edule	5290 ± 1108	Temperate/midtide to subtidal	Oxygen consumption (Newell and Bayne 1980)	van der Veer et al. 2006
Mytilus edulis	7022 ± 551	Temperate/ high intertidal to subtidal	Oxygen consumption (Gerdes 1983, Bougrier et al. 1995)	van der Veer et al. 2006
Crassostrea gigas	5722 ± 229	Temperate/intertidal	Heart rate (Widdows 1973)	van der Veer et al. 2006
Laterna eliptica	4832 ± 1306	Antarctic/shallow water (<30 m)	Oxygen consumption (Peck et al. 2002)	Agüera et al. 2017
Arctica islandica	8000	North Atlantic/subtidal to 150m	Juvenile growth rate	Ballesta-Artero et al. 2019
Perna perna	9826	Subtropical/low shore	Oxygen consumption (Tagliarolo and McQuaid 2015)	Monaco and McQuaid 2018
Mytilus galloprovincialis	10590	Subtropical/high shore	Oxygen consumption (Tagliarolo and McQuaid 2015)	Monaco and McQuaid 2018

2.6 Discussion

2.6.1 Filtration

This study showed very low filtration rates, on average 1.67 mL min^{-1} ± 0.14 SE or 0.50 ± 0.04 mL min^{-1} DW g^{-1} SE, when accounting for weight, relative to those reported for other Arctic bivalves in the literature. Although the temperature is not stated, *M. truncata* in "summer temperatures" on the shores of Vancouver Island had rates of 37.83 mL min^{-1} DW g^{-1} (Bernard and Noakes 1990). Petersen et al. (2003) reported rates for *M. truncata* in Young Sound, Northeast Greenland, between 15 and 50 mL min^{-1} over temperatures of -1.3 to 8 °C. The size of the specimens were 40-mm and 39-mm, respectively, compared to the average 58-mm of our specimens. Our results are comparable only to measured rates for *Hiatella arctica* at -1.3 °C, which range from 2 to 10 mL min^{-1} depending on food concentration (Sejr et al. 2004). The low filtration rates observed in our study may result from of the concentration of algae used. Maximum filtration rates for *H. arctica* are attained at low algal concentrations between 2000- 6000 cells mL^{-1} (equivalent to 2.5- 8 µg chl a L^{-1}) and even lower concentrations at sub-zero temperatures (Petersen et al. 2003; Sejr et al. 2004). We used concentrations of ~30 µg chl a L^{-1} and a total of upwards of 200 µg L^{-1} including phaeopigments. Indeed, the food we used was not composed of fresh phytoplankton but a stock of marine microalgae, including degraded organic matter. High concentrations of food can result in the satiation of filtering and digestive systems thus resulting in low filtration rates (Sejr et al. 2004).

In addition to this, filtration rates were not influenced by temperature in our study. Previous studies indicate that *Mya arenaria* (a temperate close relative of *M. truncata*), *H. arctica*, and *M. truncata* filtration rates all increased with increasing temperature until a certain point (Petersen et al. 2003, Riisgård and Seerup 2003). The lack of response to temperature and the low filtration rates may indicate that clams were already at their maximum food intake. Clams were fasted for two days before the feeding trial, but preliminary experiments indicated that *M. truncata* have a very long gut evacuation time, especially at low temperature, of upwards of 3 weeks (see Annexe 1). Longer fasting times, lower algal

concentrations and higher quality algae may provide more comparable results to Petersen et al. (2003) and Riisgård and Seerup (2003).

2.6.2 Oxygen consumption

Oxygen consumption rates were within the range of those found for *M. truncata* in Isfjorden, Svalbard (Camus et al. 2003). Our results are also within the range of other Arctic bivalves at similar temperatures (Table 4; Camus 2002). Differences in oxygen consumption when compared with other Arctic species may be influenced by size or the experimental method for quantifying the rate. Some studies measured the standard metabolic rate using intermittent flow respirometry over 24 hours to limit any stress or spontaneous activity, whereas we measured the routine metabolic rate, a term that describes a metabolic rate somewhere between SMR and MMR which includes a minor cost of unquantified activity (Chabot et al. 2016). *Mya arenaria* had similar rates to *M. truncata* at temperatures of 5 and 10 °C (Camus 2002; Schade et al. 2019), suggesting that this phylogenetic relationship may have a greater influence on metabolic rates than does geographic location. This has previously been demonstrated for bivalves for both metabolic rate and growth coefficients (Vladimirova et al. 2003, Saulsbury et al. 2019). Further evidence of this is that *M. truncata* had much lower rates than other examples of temperate species at similar temperatures (Ezgeta-Balić et al. 2011; Nie et al. 2018). This contradicts the metabolic cold adaption (MCA) hypothesis, which states that ectotherms in cold climates have higher metabolic rates than their counterparts from warmer climates as an adaptive strategy to compensate for short periods of favourable environmental conditions for growth, development, and reproduction (Lardies et al. 2004). However, this hypothesis has often been called into question, and studies have shown that polar bivalves often have reduced metabolic rates to conserve energy in cold temperatures with low food availability (Peck and Conway 2000, Camus 2002). The Antarctic bivalve, *Laturnula elliptica,* had very little reduction in body mass throughout the winter, which reflects low metabolic rates, allowing it to economise the use of body tissue during the period of starvation (Brockington 2001). Lardies et al. (2004) has also rejected the

MCA hypothesis for the common woodlouse, *Porcellio laevis*, with woodlice in warmer climates having higher metabolic rates than those from colder regions.

There was a clear upwards trend in oxygen consumption with increasing temperature. This is consistent with a well-documented trend in the literature for aquatic organisms (Kennedy and Mihursky 1972, Navarro and Thompson 1996, Lasota et al. 2014, Schade et al. 2019). Although oxygen consumption was greatest at 17 °C, it was also characterized by a high variance, ~50% higher than that observed for other treatments, which could suggest that it was approaching its thermal maximum. Typically, thermal maxima are represented as the temperature at which a rate peaks before decreasing. However, the eurythermal bivalve *Scapharca subcrenata* did not demonstrate a breakpoint in oxygen consumption rates at the highest temperature evaluated (32 °C) but observed increased mortality, suggesting a breakdown of the energy balance (Jiang et al. 2020). Our data did not capture an overall decrease of the rates, but the observed high variance could indicate that some individuals may support the higher temperature better than others. Furthermore, clams at 17 °C in our study showed physical signs that differed from those observed under lower temperature treatments with slow response to stimuli and hyperextended, soft siphons. Interindividual variation has been shown to increase with stress in many marine invertebrates (Petersen et al. 2003, Guscelli et al. 2019, Tanner et al. 2022). Pörtner et al. (1999) reported more erratic oxygen consumption, i.e. high variability at higher temperatures (3-4 °C compared to the -1.5 to 2 °C range that is more common for its environment) for *Limopsis marionensis*, an Antarctic bivalve, concurrent with increased mortality. The thermal maximum of 17 °C for *M. truncata*, supposed in our study considering our results, is supported by other studies. After a two-month exposure to 16 °C under laboratory conditions, *M. truncata* from Northern Scotland, which experience temperatures similar to those found in the Saint Lawrence Estuary (6-15 °C), had a reduced ability for shell repair and changes in the expression of genes related to cellular stress, immune response and biomineralization (Sleight et al. 2018). A different study, however, found a thermal maximum of 8 °C for *M. truncata* in Young Sound in Northeastern Greenland which is a more northern location than our collection site (Petersen et al. 2003). The difference in thermal tolerance could be related to where our clams

were collected and local adaptation to environmental conditions. For example, differences in thermal tolerance based on location was demonstrated in *H. arctica*, with a study revealing a greater thermal tolerance range for organisms collected near Tjärnö, Sweden (average water temperature 9.9 °C; seatemperatures.net) than for organisms collected from Young Sound, Northeast Greenland (average water temperature around 0 °C; Petersen et al. 2003). In addition, *M. arenaria* has shown a high level of plasticity with different oxygen consumption rates based on location (Lasota et al. 2014). Because our clams were collected from a southern location in the Saint Lawrence Estuary, the higher thermal tolerance may be an adaptation to a different temperature regime with temperatures reaching 16 °C.

2.6.3 Ammonium excretion

Unlike oxygen consumption, ammonium excretion was not affected by temperature. Despite not being correlated with temperature as it has been shown for other bivalves, the values observed are within the range of those reported at similar temperatures for cold water bivalves (Navarro and Thompson 1996, Pörtner et al. 1999, Brockington 2001, Stead and Thompson 2002). While these results show that this rate is not affected by temperature, it is correlated with oxygen consumption. This correlation is consistent with other studies that report ammonium excretion and oxygen consumption to vary in parallel to changes in temperature and food concentration (Pilditch and Grant 1999, Brockington 2001). Ammonium excretion rates are a proxy of catabolism and can be used to determine the breakdown of proteins which supply, among other substrates, the energy for metabolic processes (Brockington 2001). Typically, ammonium excretion is more sensitive to temperature changes than is oxygen consumption, with increased protein catabolism indicating a stress response (Pilditch and Grant 1999, Pörtner et al. 1999).

Table 4. Comparative table for bivalve oxygen consumption rates. Rates from the present study were converted to mg O_2 g^{-1} DW h^{-1} for comparison with other studies when necessary. Size is expressed as wet weight (WW), dry weight (DW) or length. For those that specified, the rate is classified as either standard metabolic rate (SMR), minimal energy expenditure required for self-maintenance, or routine metabolic rate (RMR), a rate that includes digestion and minimal movement.

Species	Location	T (˚C)	Respiration rate	Ecosystem	Average Size	Rate measured	This study at similar temperature to reference study	Reference
Mya truncata	Isfjorden, Svalbard	5.5	0.055 ± 0.02 mg O_2 g^{-1} DW h^{-1}	Arctic			0.079 ± 0.04 mg O_2 g^{-1} DW h^{-1} at 5˚C	Camus et al. 2003
Chlamys islandica	Isfjorden, Svalbard	0.5	0.064 mg O_2 g^{-1} DW h^{-}	Arctic			0.079 ± 0.04 mg O_2 g^{-1} DW h^{-1} at 5˚C	Camus 2002
Hiatella arctica	Isfjorden, Svalbard	3.5	0.094 mg O_2 g^{-1} DW h^{-1}	Arctic			0.079 ± 0.04 mg O_2 g^{-1} DW h^{-1} at 5˚C	Camus 2002
Clinocartdium ciliatum	Svalbard	0	0.075 mg O_2 h^{-1}	Arctic	16.6 g WW	SMR	0.30 mg O_2 h^{-1} at 5˚C	Schmid 1996
Chlamys islandica	Svalbard	0	0.230 to 0.513 mg O2 h^{-1}	Arctic	21.89 to 62.8 g WW	SMR	0.30 mg O_2 h^{-1} at 5˚C	Schmid 1996
Mya arenaria	Plymouth, UK	10	0.181 mg O_2 g^{-1} DW h^{-1}	Temperate			0.126 ± 0.063 mg O_2 g^{-1} DW h^{-1} at 11˚C	Camus 2002
Mya arenaria	Schnatermann, German Baltic coast	5	0.07 mmol O_2 d^{-1} g^{-1}	Temperate	277 mg DW	SMR	0.059 mmol d^{-1} g^{-1} DW at 5˚C	Schade et al. 2019
Mya arenaria	Chesapeake Bay, Maryland, USA	5	0.01 mmol O_2 d^{-1} g^{-1}	Temperate	277 mg DW	RMR	0.059 mmol d^{-1} g^{-1} DW at 5˚C	Kennedy and Mihursky 1972 (as referenced by Schade et al 2019)
Mya arenaria	Eastern Passage, Nova Scotia, CA	5	0.27 mmol O_2 d^{-1} g^{-1}	Temperate	277 mg DW		0.059 mmol d^{-1} g^{-1} DW at 5˚C	Emerson et al. 1988 (as referenced by Schade et al 2019)
Modiodiolus barbatus	Mali Ston Bay, Croatia	9	20.89 µmol h^{-1} g^{-1}	Temperate/ subtropical	5.4 ± 0.5 cm.	RMR	3.94 µmol h^{-1} g^{-1} at 11˚C	Ezgeta-Balić et al. 2011
Modiodiolus barbatus	Mali Ston Bay, Croatia	15	~16.5 µmol h-1 g-1	Temperate/ subtropical	5.4 ± 0.5 cm.	RMR	4.99 µmol h^{-1} g^{-1} at 14 ˚C	Ezgeta-Balić et al. 2011
Dosinia coorrugata	Dalian, China	10	0.894 mg g–1 h–1	Temperate	6.16 g DW		0.126 ± 0.063 mg O_2 g^{-1} DW h^{-1} at 11˚C	Nie et al. 2017

2.6.4 Calcification

Although net calcification has been reported to be positively correlated with temperature in bivalves, the results for *M. truncata* did not follow this trend (Schöne et al. 2005, Mancuso et al. 2019). *Arctica islandica*, another long-lived Arctic bivalve, had optimum shell growth between 12 and 17 °C, with temperature and food availability representing the two most important factors for shell growth (Schöne et al. 2005). That such a relationship with temperature was not observed in the present study may be due to the slow growth rate of *M. truncata*, however the results were not null, suggesting that rates were recorded. *Mya truncata* initially grows quickly but growth rates decrease with age, as documented in many different locations (Petersen 1978, Hewitt and Dale 1984, Vieweg et al. 2012). In this study, we did not detect a significant difference in shell length over the 5-month period the clams were in the laboratory, (average -0.41 mm ± 1.01 SD, n = 300), suggesting that the clams used may have been in the slower growth phase associated with older individuals. However, the age of the clams was not quantified as part of our study. A lower net calcification with older individuals has also been noted in the striped venus clam, *Chamelea gallina* (Mancuso et al. 2019). Calcification in bivalves has also been shown to be influenced by circadian, tidal, and seasonal patterns (Schöne et al. 2005). For example, the blue mussel, *Mytilus edulis* can shift to higher calcification rates during the day when macrophytes regulate the pH more effectively, mitigating effects of acidification (Wahl et al. 2017). *Arctica islandica* has reduced shell growth during the fall when spawning occurs and in winter, perhaps associated with food scarcity (Schöne et al. 2005). This study was conducted for only 2-5 hours at mid-day in late spring which may not have captured the period of high calcification. Further studies should look to identify potential circadian and seasonal variations and to capture low calcification rates more accurately.

2.6.5 Thermal sensitivity

Aerobic metabolism, which is directly influenced by temperature in aquatic ectotherms, supplies energy to fulfill an animal's needs and is a fundamental mechanism by which an animal may respond to climate change (Schulte 2015). Higher thermal sensitivity is

associated with organisms with lower tolerance to temperature variation (Gilchrist 2000). High thermal sensitivity allows organisms to react faster to temperature changes, although the trade-off is that they quickly reach the limit of their capacity to supply the energy required to sustain higher rates, creating an energy imbalance. *Pyganodon grandis*, a subarctic mussel, has a higher thermal sensitivity than the closely related temperate mussel, *Pyganodon fragilis*. It may allow *P.grandis* to grow faster to take advantage of the shorter summer window but may reflect enhanced stenothermy (Doucet-Beaupré et al. 2010). T_A is a proxy of this thermal sensitivity with increasing values indicating greater thermal sensitivity. In bivalves, the reported T_A ranges from 4832 to 10590 with an average of 7112 (Table 3). The T_A calculated for *M. truncata* in our study (3598 considering all the values measured) is below values reported for bivalves, being close to T_A calculated for *L. elliptica*, another polar species. However, T_A in bivalves does not seem to follow any geographic trend. Cold adapted species are generally more sensitive to increasing temperatures (Gilchrist 2000). This is not the case, with the Antarctic bivalve *L. eliptica* having one of the lowest T_A yet described (Agüera et al. 2017). Another factor influencing the T_A could be the nature of a bivalve's environment. For prawns, species inhabiting more variable thermal environments have higher sensitivity to temperature when compared to species in more stable thermal conditions, which may allow them to compensate for temperature increase by increasing their metabolism to a greater extent (Magozzi and Calosi 2015). This contrasts the hypothesis that intertidal organisms and other environments with highly fluctuating variables may be expected to have lower thermal sensitivity because of the high fluctuations in their temperature and therefore having more general and less adapted enzymes (Kooijman 2000). However, environmental fluctuations do not seem to explain the differences in T_A shown in the literature. Our data for oxygen consumption did not capture the expected drop in performance at high temperatures, and so all five temperatures were used to calculate a relatively low T_A of 3598. As in theory, T_A represents the linear part of the thermal performance curve, if the 17 °C treatment represents the point at which the curve levels off, then only the first four temperatures are used, yielding an T_A of 5159, which is more within the range of values reported in the literature. Using only the three lowest temperatures, T_A

continues to increase to 6349. The question is thus, which is the real value? Van der veer (2006) suggests that T_A are similar between similar species, and what changes are the thermal limits. In their study, the authors chose to average T_A to 5800 for the five bivalve species they studied. Indeed, T_A calculated by van der Veer (2006) were similar, between 5290 to 7052, however other studies have shown a much larger variation. This may reflect differences in calculations rather than differences in thermal sensitivities. In theory, with our data there is no statistical differences between T_A because of the high variability around the means observed for each individual but could make a difference in a modelling setting such as when using DEB. Although many articles have run sensitivity analyses on the primary parameters of DEB models (Ren and Ross 2001, Monaco et al. 2014, Matyja 2023), T_A remains less tested despite its importance in understanding the effect of changing temperatures (Carvalho-Silva et al. 2019). This would be interesting to investigate, especially considering the maintenance coefficient that describes the temperature effect on metabolism is particularly sensitive in the Pacific oyster, *Crassostrea gigas* (Ren and Ross 2001).

2.6.6 Conclusion

Overall, results displayed high levels of variability between and within physiological rates in response to temperature. Data suggests that 17 °C is approaching the thermal maximum of *M. truncata*. However, it is important to note that results were quantified on individuals from a southern location of *M. truncata* species distribution and that other populations, especially from more northern locations, may deviate from this value because of local adaptation. Often, warm-edge populations are most vulnerable to temperature changes because they live closer to their thermal limits (Bennet et al. 2019). This may be true for *M. truncata* in the Saint Lawrence Estuary because coastal bottom temperatures can reach a maximum of 15-16 °C in the summer (C. McKindsey, personal communication). However, to fully understand the vulnerability of *M. truncata* to temperature changes it would be important to study other populations of *M. truncata* and the effect of temperature on reproduction because lower recruitment has been observed at higher temperatures (Beukema et al. 2009, Thomas and Bacher 2018), something that has already been reported for *M. truncata* in the Southern North

Sea (Amaro et al. 2003). In addition, further understanding the within-species thermal limit variation from different populations would be important to properly assess the effect of temperature on *M. truncata*.

CONCLUSION GÉNÉRALE

3.1 RÉSUMÉ DES RÉSULTATS

Une connaissance de la physiologie des espèces arctiques est souvent manquante bien qu'elles soient en première ligne du changement climatique. Cela est vrai pour la mye tronquée, *Mya truncata*. Des quatre taux physiologiques mesurés c'est-à-dire filtration, consommation d'oxygène, excrétion d'ammonium et calcification, seule la consommation d'oxygène montrait une tendance croissante face à une augmentation de température. Les taux de filtration dans notre étude étaient plus bas que d'autres rapportés dans la littérature pour des bivalves arctiques, et ne montraient aucun changement avec la température, peut-être à cause d'un phénomène de satiété liée aux concentrations d'algues utilisées. La consommation d'oxygène était concordante avec des études précédentes pour *M. truncata* et autres bivalves arctiques. Une grande variance à 17 °C pourrait indiquer que cette température s'approche du maximum thermique, ce qui est soutenu par des signes visuels de stress comme un siphon en hyperextension. L'excrétion d'ammonium n'était pas influencée par la température, mais était similaire aux taux mesurés pour d'autres bivalves vivants en eau froide. Nos expériences n'ont pas capté une différence de taux de calcification avec la température. Une plus longue période d'incubation permettrait potentiellement mieux capter un taux de calcification faible chez une espèce comme *M. truncata* avec un lent taux de croissance à l'âge adulte.

3.2. LIMITATIONS ET AMÉLIORATIONS

Notre projet était conçu avec le but de pouvoir faire des expériences en milieu isolé dans le Nord canadien, dans des communautés qui n'ont pas d'infrastructure expérimentales. Certaines limitations de notre étude sont donc liées aux conditions attendues auxquelles nous aurions dû faire face en milieu isolé. La durée d'acclimatation de deux semaines a

volontairement été gardée la plus courte possible pour être capable de mener une expérience complète convenant à la longueur des séjours dans le Nord qui sont souvent limitée à quelques semaines. Le système expérimental qu'on a utilisé a été créé pour être portable et fonctionner avec une source d'électricité limitée. Les capacités de refroidissement de l'eau étaient donc contraintes par la puissance de la thermopompe. De plus, la construction du système a pris plus de temps qu'anticipé (notamment à cause de la pandémie) et ne nous a pas permis de faire l'expérience durant la période hivernale durant laquelle l'eau est la plus froide. Ainsi nous n'avons pas pu tester des températures plus faibles que 5 °C, près de la limite froide de l'espèce. À cause de la pandémie, l'expérience prévue dans le Nord à Kuujjuarapik, QC, n'a pas pu être réalisée et nous avons eu recours à des myes provenant de l'estuaire du Saint-Laurent.

Quelque chose qu'on a remarqué était une grande variabilité interindividuelle dans les taux. La variabilité est attendue, mais n'a parfois pas permis de détecter des différences statistiques avec les tests non paramétriques utilisés. Quelque chose à essayer dans le futur est de mesurer le taux initial pour chaque individu avant d'augmenter la température, ensuite de comparer la différence entre le taux initial et le taux aux températures d'exposition du même individu. Cela pourrait diminuer l'effet de la variabilité interindividuelle et isoler l'effet de la température sur les taux physiologiques individuels. De plus, on pourrait augmenter la taille des échantillons pour s'assurer que les résultats obtenus sont une réflexion de la réalité.

Les méthodes pour mesurer le taux de filtration pourraient être améliorées. Pour éviter de saturer l'estomac et les branchies, on pourrait allonger la période de jeûne et diminuer les concentrations d'algues initiales. À cause d'un manque de matériel, on a seulement pris des mesures au début et à la fin de l'incubation. Pour mieux comprendre les taux de filtration, on pourrait échantillonner l'eau à plusieurs instants pendant l'incubation. Cela nous permettrait d'identifier et d'analyser des changements des taux individuels au cours du temps. Utiliser des algues d'une meilleure qualité serait aussi importante pour des résultats plus comparables à la littérature.

3.3. LA MODÉLISATION : UNE PROCHAINE ÉTAPE

Les projections de distribution d'espèces sont un aspect d'intérêt dans la recherche des effets des changements climatiques, particulièrement dans un contexte de gestion (McKenzie et al. 2016). Les modèles basés sur la physiologie peuvent établir un lien entre les fenêtres de tolérance, les conditions environnementales et les habitats adéquats pour une espèce (Teal et al. 2018). L'un de ces modèles est le modèle Dynamic Energy Budget (DEB). Le modèle DEB est un modèle bioénergétique qui permet de modéliser les processus d'acquisition de l'énergie et de son utilisation pour l'entretien de la biomasse, le développement, la croissance et la reproduction (Koojiman 2000). Le théorie DEB permet d'établir des liens entre les processus métaboliques d'un organisme tout au long de son cycle de vie en fonction de la température et de la disponibilité en nourriture. Cette théorie se base sur les principes de la conservation de masse des éléments, la thermodynamique et l'homéostasie, c'est à-dire un équilibre dynamique des variables clés autours de valeurs bénéfiques et optimales pour le fonctionnement de l'organisme. Le modèle DEB utilise le concept d'une réserve qui permet de prendre en compte des périodes où un organisme utilise de l'énergie mais n'en consomme pas, par exemple durant le stade embryonnaire et les périodes de jeûne (Koojiman 2000). Les sorties du modèle DEB nous permettent de décrire des fonctions importantes d'un organisme (comme la croissance, la reproduction ou le registre aérobie) à une température et une disponibilité de nourriture donnée. Il est possible, donc, de coupler ces résultats avec des projections environnementales pour faire des prédictions sur la distribution d'une espèce (Teal et al. 2018). Teal et al. (2012) ont utilisé cette approche pour modéliser l'effet des changements climatiques sur la croissance potentielle des poissons *Pleuronectes platessa* et *Solea solea*. Les résultats de cette étude étaient en accordance avec les changements de distributions saisonniers et ont prédit que les *P. platessa* juvéniles auront un déplacement au large dû à une réchauffement important des zones côtières. Les avantages de l'utilisation du modèle DEB pour prédire la distribution incluent la prise en compte de tous les stades de vie d'un animal et l'application aux espèces

où les données empiriques ou expérimentales sont rares. Le modèle DEB se base sur l'idée que le métabolisme de tous les organismes vivants fonctionne de la même façon (Koojman 2000). Pour cette raison, on peut estimer les paramètres du modèle en utilisant des paramètres d'autres organismes, et on peut utiliser des données issues de la littérature et du laboratoire pour développer un modèle. Steeves et al. (2018) ont utilisé la température de la surface de la mer issue d'un modèle à haute résolution du climat comme une forçage dans les modèles DEB pour *Crassotrea virgica* et *Mytilus edulis* pour comparer la performance des bivalves sur trois différentes périodes (1986-1990, 2016-2020, et 2046-2050). Lavaud et al. (2021) ont fait une revue de littérature sur le rôle de DEB dans la physiologie de conservation en citant son utilité pour aborder des défis de maintenir la biodiversité, assurer la survie d'espèce, l'écotoxicologie et le fonctionnement des écosystèmes face à des changements environnementaux.

La paramétrisation initiale d'un modèle DEB utilise des données zéro-variées (Tableau 4) et uni-variées pour estimer les paramètres du modèle. Les données zéro-variées sont scalaires et représentent un temps statique dans le développement de l'organisme, par exemple, l'âge à l'éclosion, l'âge et/ou longueur à maturité et la durée de vie, tous à une température donnée. Les données uni-variées sont des taux qui peuvent être influencés par des facteurs externes, comme la température ou la disponibilité en nourriture. Avec ces données, le programme estime les paramètres itérativement pour s'aligner le mieux que possible avec les données empiriques. S'il manque l'information requise pour l'estimation de paramètres, la méthode covariable estime les paramètres en utilisant les paramètres d'un animal « général » ou d'une espèce relativement proche.

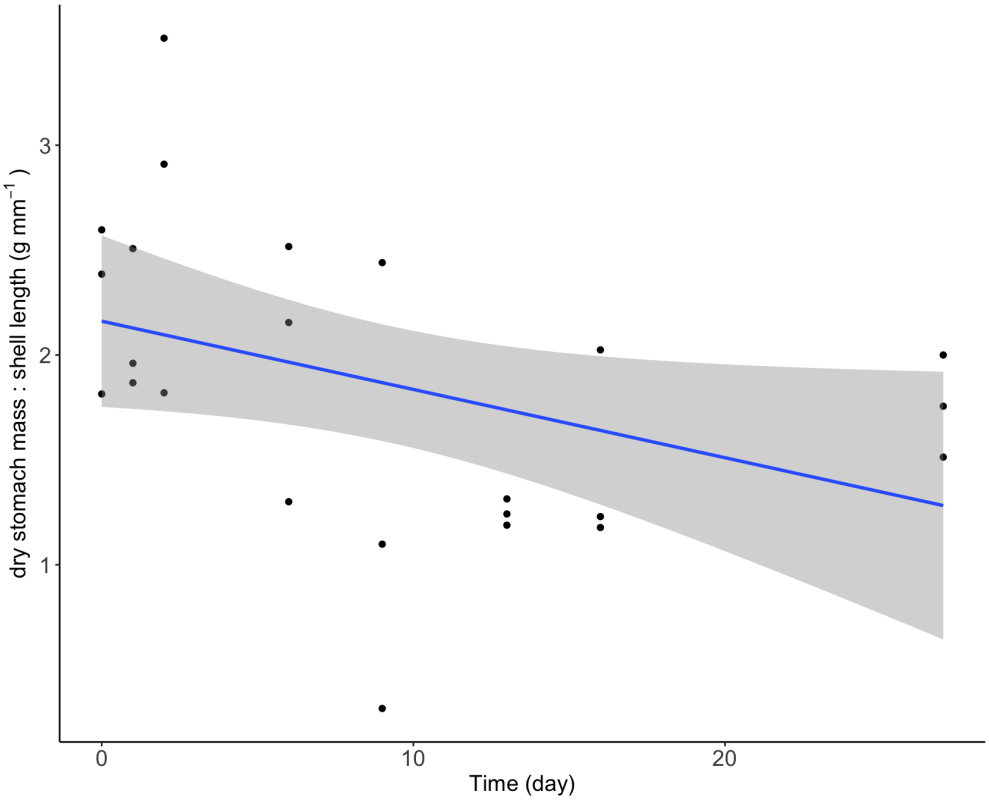
La tolérance et les limites thermiques sont des paramètres que le modèle DEB ne peut pas estimer à partir de l'animal général (Teal et al. 2018). Pour pouvoir inclure ces paramètres dans le modèle, qui est l'un des aspects cruciaux qui détermine les changements de distributions de plusieurs espèces, il faut avoir ou acquérir cette information pour chaque espèce. Mon travail de maitrise c'est concentré sur l'acquisition de ces paramètres constitue donc un travail préliminaire de grande importance pour le développement futur d'un modèle

DEB pour *M. truncata*. De plus, Kooijman (2000) émet la supposition que tous les taux physiologiques varient de la même façon avec la température. Cela fait que le modèle généralisé inclue seulement une valeur pour expliquer le changement de taux que ça soit pour la consommation d'oxygène ou la filtration. L'acquisition de données pour chaque taux physiologique représente ainsi un avancement pour la paramétrisation du modèle. Le modèle DEB utilise la température d'Arrhenius pour intégrer les effets de la température dans les sorties du modèle. Van der Veer (2006) suggère que la consommation d'oxygène est la plus utile pour calculer la température d'Arrhenius. Cependant, les physiologistes se questionnent sur ce point parce que ça ne prend pas en compte la complexité des processus qui gouvernent ces taux. Nos résultats confirment que les taux physiologiques ne varient pas de la même façon avec un changement de température. Ça pourrait être important d'inclure plusieurs températures d'Arrhenius si on vise à estimer plusieurs taux et réponses avec un modèle DEB.

Tableau 4. Les données zero-variées de *Mya truncata*. Les données zéro variées sont scalaires et représentent un temps statique dans le développement de l'organisme à une température donnée. Certaines données sont tirées de *M. arenaria* lorsque manquante pour *M. truncata*.

Paramètre	Description	*Mya truncata*	*Mya arenaria*	Source
ab	Âge lorsque l'organisme commence à s'alimenter		2 jours	Flyanchinaskaya and Lezin 2017
ap	Âge à la puberté	3-6 ans		Petersen 1978
am	Âge maximale	62 ans		Siferd 2005
L	Longueur de la coquille à la métamorphose	0.27-0.36 mm		Muus 1973
Lp	Longueur de la coquille à la puberté	20 mm		Petersen 1978
LR	Longueur de la coquille à la maturité sexuelle	31 mm (male) 32 mm (femelle)		Wood 2022
Li	Longueur ultime	100 mm		Manore et al. 2020; Amaro et al. 2003
Wwi	Masse humide ultime	166.8 g		Manore et al. 2020
N	Nombre de progéniture possible		120 000 ovules par an	Brousseau 1978

ANNEXE



Annexe 1. Preliminary experimental data for gut evacuation in *M. truncata*. Clams were kept at 3 °C with no food. Three clams were sampled on each sampling day. Each was measured, the stomach was dissected, and the stomach tissue dried for 24 hours. The slope of the regression line of dry stomach mass: shell length vs time is -0.033.

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