Same mesozooplankton functional groups, different functions in three Arctic marine ecosystems

Saint-béat B. [1, 2, *], Darnis G. [3], Leclerc M. [2], Babin M. [2], Maps F. [2]

[1] IFREMER, Dyneco Pelagos BP Plouzané, France
[2] Takuvik Joint International Laboratory Université Laval (Canada) – CNRS (France), Département de biologie et Québec-Océan, Université Laval, Quebec CA ,France
[3] Québec-Océan, Département de biologie Université Laval Québec ,Canada

* Corresponding author : B. Saint-Béat, email address : blanche.sintbeat@gmail.com

Abstract :

1. The trophic relationships interconnecting marine organisms together into a dynamic trophic network drive the structure and the functioning of the entire ecosystem. Since the flow of carbon within trophic networks is controlled by a variety of functional traits related to food acquisition and individual survival, it is crucial to understand how functional diversity relates to marine ecosystems properties such as the resistance and resilience against perturbations.

2. In the Arctic, marine ecosystems are facing stronger and faster environmental changes than anywhere on Earth, leading to profound perturbations in the planktonic assemblages at the base of the trophic networks. While it is known that mesozooplankton plays a crucial role of matter and energy hub within marine Arctic food web, the precise role of the diverse mesozooplankton functional groups in carbon circulation and in marine ecosystems functioning remains poorly known.

3. We coupled a trait-based approach of mesozooplankton diversity to an ecological network analysis approach to test whether similar mesozooplankton functional groups played similar ecological roles in three Arctic ecosystems during the summer period. We formed nine mesozooplankton functional groups by gathering different species according to their feeding strategies. Then we implemented those into inverse food web models (LIM) describing three contrasted Arctic ecosystems. In each ecosystem, we performed sensitivity analysis experiments where each mesozooplankton functional group was removed one at a time.

4. Our results showed that, although the same main functional groups composed the three ecosystems, the few outstanding changes observed in the carbon circulation within the food web were strongly controlled by both the initial whole-network properties and productivity of the ecosystem.

5. The various roles played by a given mesozooplankton functional group in the ecosystem depend on its impact on carbon flows through the food web it belongs to. As a result, identifying which functional groups could be threatened, and which carbon flows could be altered by climate change is critical information to predict future ecosystems functioning.

Introduction

Despite all the complexity and diversity of marine ecosystems, their structure and functioning can be considered as emerging properties of networks of interactions between organisms. From its fixation into organic matter (e.g., photosynthesis) to its possible export out of the system (e.g., as inorganic by-product of metabolism, by burial into sediments, etc.), carbon is distributed within trophic networks according to biological functions controlling its acquisition, usage, and accumulation (Schmitz and Leroux, 2020). These diverse biological functions belong to the broader category of "functional traits", which are defined as any morphological, metabolic and behavioural property that impacts an individual's fitness via its effects on growth, reproduction, and survival (Violle et al., 2007). While functional traits are very diverse, the combinations they are effectively forming within organisms are much fewer.

Organisms sharing similar functional traits form coherent "functional groups" whose interactions structure the trophic network and control its activity. Essential ecosystem functions, such as carbon fixation and export or its ability to maintain its state when facing to external perturbations, emerge from these trophic networks' properties. As a result, functional grouping has increasingly been used as an efficient way to link community ecology to biogeochemical processes, and biodiversity to ecosystem functioning, especially in aquatic ecosystems (Martini et al., 2021). The functional traits approach simplifies the definition of zooplankton ecological niches (Benedetti et al., 2018). For instance, while the abundance of any given species could fluctuate randomly within their own functional group envelope over time, the total abundance of each functional group can be predicted in response to environmental forcing (Mutshinda et al., 2016). Functional groups based on species sharing similar functional traits related to food acquisition and use (metabolism) enhance the

generality and predictability of conclusions about how functional diversity controls marine ecosystems functions (e.g., (Kiørboe et al., 2018; Saint-Béat et al., 2015).

This feature appears critically important when studying Arctic marine ecosystems, since they have been undergoing radical changes in the wake of the fastest and strongest warming on the planet of the last decades (AMAP, 2019). One overarching driver of changes in Arctic marine ecosystems is the alteration of the sea ice cover extent, thickness and the timing of freezing and thawing. Several studies documented the linkages between these significant changes in the sea ice dynamics and changes in phytoplankton assemblages, spring bloom phenology and duration (Arrigo and van Dijken, 2015; Bélanger et al., 2013; Blais et al., 2017; Li et al., 2009). Moreover, the highly specialized Arctic species are threatened by the strength and speed of environmental changes on one hand, and the increasing presence of temperate-associated species on the other hand. As a result, Arctic marine ecosystems will face significant changes in their structure and functions in response to expected changes in species compositions (e.g., (Frainer et al., 2017; Kortsch et al., 2015; Renaud et al., 2018). However, the consequences of these changes on the ecosystem functioning as a whole have only recently started to be explored (Saint-Béat et al., 2020; Saint-Béat et al., 2018).

Within Arctic marine ecosystems, mesozooplankton forms a heterogeneous group of metazoan species that are characterized by various traits conferring them efficient and unique adaptations to this harsh environment. Mesozooplankton is often long-lived (individuals can survive for several years) and forms a crucial hub of matter and energy between the phytoplankton and early life-stages of predator species (e.g., fish larvae) or adult forage species that are the staple of these predators (Darnis et al., 2012). Mesozooplankton is more important in Arctic ecosystems than elsewhere because the new primary production is concentrated within the short summer season. Its

crucial role is largely supported by the various feeding strategies that mesozooplankton species have developed. The successful feeding strategies involve combinations of morphological (e.g., appendages) and behavioural (e.g., swimming and filtering activity) adaptations that can be classified into four distinct groups split into two categories: *ambush* strategies (active ambush and passive ambush) and *active* strategies (current feeding or cruising)(Kiørboe et al. 2011). In general, an active feeding strategy generates hydromechanical perturbations in the surrounding medium that leads to higher encounter rates with preys (higher gain) but also with predators (higher loss), when compared to ambush feeders (Almeda et al., 2017; van Someren Gréve et al., 2017). Ambush feeders detect hydromechanical signals generated by motile preys (Kiørboe, 2011). Active ambushers then actively attack and capture its preys, while passive ambush feeders passively catch it upon its detection. In any case, ambush feeders remain still and are rather inefficient at collecting non-motile preys (Almeda et al., 2018). Among active feeders, feeding-current feeders generate a current to channel potential preys and either catch them through a filtering structure or pick them up on detection (Kiørboe, 2011), while cruisers actively explore the waters to encounter their preys (Kiørboe, 2011). Since the different feeding strategies of mesozooplankton strongly influence the trophic relationships between mesozooplankton organisms, their preys and their predators, they are functional traits that may control the flows of carbon within Arctic marine food webs and the resulting ecosystem functions.

Unravelling the role of the distinct mesozooplankton functional groups in the control of carbon flows within the food web is a first step towards a better understanding of the fate of marine ecosystems in a rapidly changing Arctic Ocean. In this study, we test the following hypothesis about Arctic planktonic trophic networks: each functional group has generic ecological functions and its removal alter the functioning of distinct ecosystems in the same ways. We applied a trait-based approach to define the functional groups forming the nodes of trophic network models, for

three contrasted Arctic marine ecosystems: the Amundsen Gulf, and the Western and the Eastern Baffin Bay. We performed a sensitivity analysis consisting of removing one functional group at a time to explore the responses of each trophic network to the resulting perturbations. First, the impacts of the removal on ecosystem functioning were revealed by ecological network analysis (ENA) and then the reorganisation of carbon circulation was described by detailed analysis on trophic pathways.

Materials and methods

Ecological modelling and ecological network analysis (ENA)

Ecological network analysis (ENA) is an analytical tool to study groups of organisms as part of the connected trophic network they belong to. It generates a set of whole-network metrics that expose the nature of the relationships between trophic groups resulting from both direct and indirect interactions (Fath and Patten, 1998) and reveal the emerging properties such as the recycling and the retention of carbon, or the organization level of the ecosystem (e.g. Nogues et al., 2021; Saint-Béat et al., 2020). Network analysis is based on a weighted, directed and balanced trophic network, whose currency is usually carbon content (Borrett and Lau, 2014).

The linear inverse modelling approach (LIM) is used to complement datasets and close the carbon budget. A random sampling procedure (Van den Meersche et al., 2009) allows for density probability function to be computed for all possible solutions for each simulated flow (Van Oevelen et al., 2010). This study focused on three Arctic ecosystems that were previously described by LIM procedure: the Amundsen Gulf (Forest et al., 2011; Saint-Béat et al., 2018), the eastern and western Baffin Bay (Saint-Béat et al., 2020), a description of these ecosystems is available in supporting information (Appendix S1).

Original LIM models of the three contrasted arctic ecosystems

The periods covered by each original trophic network model varied. On one hand, the two Baffin Bay models (Saint-Béat et al., 2020) represented the trophic networks in its eastern and western parts for conditions observed during June 2016. Each side corresponded to distinct phases of the seasonal phytoplankton bloom. The bloom was starting in the western Baffin Bay where sea ice

still present, whereas it was much advanced in the eastern Baffin Bay where the sea ice cover had melted already. On the other hand, the Amundsen Gulf model simulated the processes sampled during the whole seasonal phytoplankton bloom of 2008 (Saint-Béat et al., 2018).

The original models were designed in accordance with the most recent knowledge of each ecosystem. While we attempted to standardize the three food web models, it is important to note that biological processes sampled in each ecosystem were not exactly the same. This impacted the topology of each model, especially the number of groups of primary producers and mesozooplankton considered (Fig. 1), as well as the kind of constraints used to limit flow values in each model (Table S1). Regarding primary producers, the small (SPH) and large phototrophs (LPH) groups were considered in the Amundsen Gulf model, whereas both Baffin Bay models integrated only one phytoplankton group (PHY), with the addition of a sea-ice algae group (SIA) in the still sea-ice covered western Baffin Bay model only. It is important to note that, in the Amundsen Gulf, the sea ice algae were included in the both phototroph groups, since primary production was measured for the upper water column without distinguishing production of phytoplankton or suspended sea ice algae. In the western Baffin Bay however, the sea ice algae production measurements allowed to consider them in a distinct compartment. Mesozooplankton was split according to the type of prey consumed for Baffin Bay models, or taxonomic criteria for the Amundsen Gulf. Then, in each model one compartment represented microzooplankton (MIC), bacteria (BAC), and Arctic cod (*Boreogadus saida*) larvae (BSL). Two compartments represented detritus, one for particulate detritus (DET) and another for dissolved organic detritus (DOC). Carbon left the system either by respiration for all living compartments or export. Export corresponded to carbon not consumed within the trophic network: for consumers (micro- and mesozooplankton, and Arctic cod larvae) it represented the carbon consumed by predators not implemented in the model. A second kind of export, representing two processes including in the

carbon biological pump (Boyd et al., 2019) was also implemented in all models: the sinking of particles and the seasonal active transport of lipids by *Calanus* spp..

LIM models constrain carbon input into the trophic network via *in situ* measurement of primary production. This input for the considered period was equal to 52.5 g C m^{-2} in the Amundsen Gulf model (it corresponded to a monthly production equal to 17.5 g C m^{-2}), whereas it was 18 and 20.5 g C m^{-2} month^{-1} in the eastern and western Baffin Bay, respectively. Bacterial production and bacterial growth efficiency that control the use of dissolved organic carbon and production of recycled carbon available for transfer to higher trophic levels, were constrained by *in situ* measurements in all three models. Exudation and viral lysis, that have been shown to be crucial for marine ecosystems functioning (Saint-Béat et al., 2018), were constrained too. Potential carbon loss by particles sinking and seasonal migration were constrained in all models. Carbon export via seasonal migration was limited considering a potential reserve accumulation ranged between 70% of the minimal and maximal biomass of stages above copepodite IV. In the Amundsen Gulf model only, herbivory by both micro- and mesozooplankton, bacterivory by microzooplankton and total mesozooplankton respiration were constrained by experimental data.
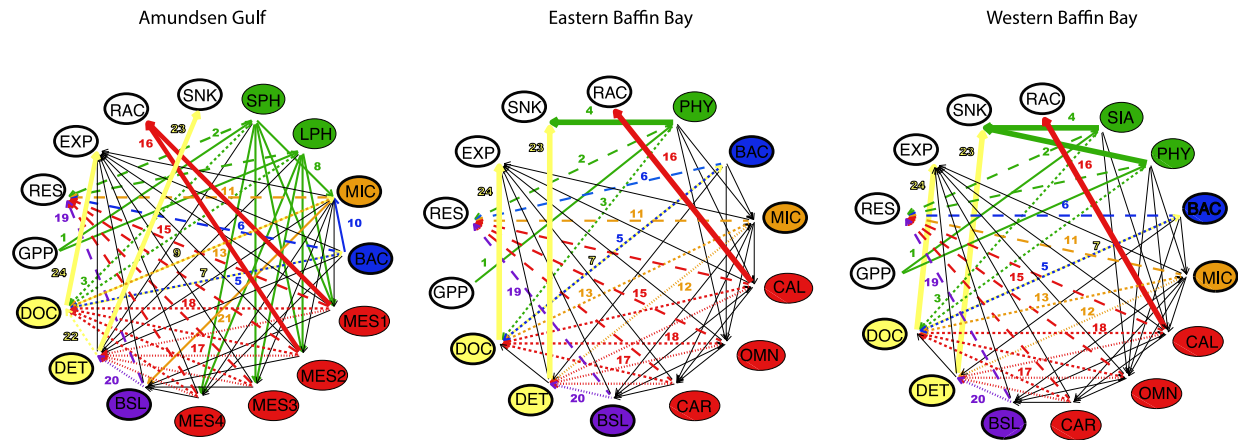
Figure 1. Food web diagram of Amundsen Gulf, the eastern and western Baffin Bay. Coloured circles represent internal compartments, green for primary producers (SPH and LPH = small < 5 *μm* and large phototrophs > 5 *μm*, respectively, SIA for sea ice algae and PHY for phytoplankton), blue for bacteria (BAC), orange for microzooplankton (MIC), red for mesozooplankton (CAL = herbivorous Calanus spp., OMN = Omnivores, CAR = Carnivores), purple for Arctic cod larvae (BSL) and yellow for detritus (DET and DOC for particulate and dissolved detritus, respectively). The black bordered circles correspond to compartments common to all models. White circles correspond to external connections: respiration (RES), gross primary production (GPP), export (EXP), sinking (SNK), lipids accumulation (RAC). Black flows are not constrained by the data listed in Table S1 in supporting information. The colour of the arrows and identification numbers of each flow refers to its source. Full lines represent predation/grazing, thick full lines represent carbon export, thick dashed lines refer to respiration, short dashed lines represent exudation/excretion and dotted lines are for egestion.

Mesozooplankton functional groups

In this study, we modified the three original models presented above by considering a different way to represent the wide mesozooplankton diversity. In the *new* models, mesozooplankton behavioural traits defining their feeding strategy: passive or active ambush feeders, cruiser and current feeders, were combined to the type of prey consumed (Table S2). The combination of

feeding strategies and the type of prey consumed split mesozooplankton taxa into nine functional groups (Table S3). Some functional groups were much more diverse than others.

The four original groups were replaced by 9 functional groups (presence of passive ambush carnivore) in the Amundsen Gulf model, whereas the three original Baffin Bay mesozooplankton groups increased to 8 functional groups (Table S3). This led us to consider a higher number of prey-predator links within mesozooplankton. Discussions with Arctic mesozooplankton experts and a thorough examination of the literature allowed us to identify all known links between functional groups. Thus, the total number of trophic pathways increased from 65 to 114 for the Amundsen Gulf model, whereas in Baffin models it went from 49 to 93 and from 55 to 103 for the eastern and western Baffin Bay models, respectively. These new flows were bounded using the information that limited mesozooplankton flow values in the original models. In situ abundances of each species stage (Table S4, S5 and S6), converted into carbon biomass according to empirical relationships between prosome length and carbon content, were used to bound loss of carbon by respiration, carbon production and carbon consumption of each species using allometric relationships (Moloney and Field, 1989). Respiration, consumption and production of each functional group were defined as the sum of values calculated for each species composing the group. The constraints defined for others trophic groups remained unchanged in the new models.

Role of the various functional groups in arctic marine ecosystem functioning

To explore the relative importance of each of the 9 functional groups defined above, we designed sensitivity analysis experiments in which food web models were altered by removing one particular functional group at a time. Control models contained all the functional groups whereas

in each degraded model a single functional group and its associated flows were removed. Thus 28 distinct runs were performed: three control model runs; one for each ecosystem, and 25 degraded model runs; 8 for the eastern and western Baffin Bay, and 9 for the Amundsen Gulf. LIM estimated the flow values of altered food web and ENA quantified various attributes of the food web as well as the nature of relation between feeding groups. The LIM calculated 50,000 likely solutions for each unknown flows and hence we obtained 50,000 distinct possible food webs for each run. Each of them was submitted to ENA in order to define the range of values for each network emergent properties. The LIM and network analysis were performed using limSolve package version 1.5.6 (Van Oevelen et al., 2010) and netIndices R package 1.4.4 (Kones et al., 2009), respectively.

Ecosystem network analysis indices

We characterized the trophic network functioning by computing six ENA indices:

1- The average Compartment Throughflow (TSTbar) corresponding to the mean activity per compartment: TSTbar measures the average quantity of carbon flowing through any compartment.

2- The average mutual information (AMI) measuring the specialisation of trophic pathways: it estimates the average amount of constraint exerted on an atom of carbon to flow from any one compartment to the next one (Ulanowicz, 1986), higher AMI meaning more constrained carbon and more specialised pathways.

3- Average path length (APL) corresponding to the mean number of compartments visited by an atom of carbon between its entry and exit of the system (Kay et al., 1989): this is a proxy of the

carbon retention within the ecosystem. Higher APL suggests longer food chains and higher retention.

4- Finn cycling index (FCI) measuring the proportion of carbon atoms involved in loops: higher FCI means more carbon re-use before its eventual loss outside the system.

5- Relative Ascendency (A/C), a ratio between 0 and 1 describing the level of organization reached by the system (Ulanowicz, 1986; Ulanowicz, 1997): a higher A/C means a higher specialisation of the pathways.

6- The compartmentalization (Cbar) index revealing the degree of connectedness of the various subsystems: a value of 0 means only one system exists, whereas a value of 1 suggests that several loosely connected subsystems share the carbon flows (Latham, 2006).

This set of indices was calculated for the 50,000 solutions proposed by the LIM procedure in order to assess the uncertainty associated with each index. A multivariate statistical analysis, a PCA (Principal Component Analysis), was performed of the mean values of ENA indices previously described, with FactoMineR version 2.4 (Lê et al., 2008) and factoextra R-Cran packages version 1.0.7.

Then, the mean involvement of each functional group was calculated. It corresponds to the proportion of the carbon flowing the trophic pathways, which enters and exits a functional group. The impacts on carbon circulation were investigated through i) the analysis of the contribution of each source to the sink diet and ii) the analysis of compartment dependency. Whereas contribution of each sources focuses only on direct trophic links, the dependency index consider both direct and indirect pathways (Szyrmer and Ulanowicz, 1987). The contribution of each source to i) the diet of grazers, ii) the diet of predators, iii) detritus in presence and in lack of each functional group was calculated for each of the 50,000 flows solutions and compared. Dependency allows tracking the

origin of the carbon consumed/received by each compartment. A higher dependency on a source means that more carbon directly or indirectly flows from that source to the sink. Consequently, the dependency of the compartment that was removed in the degraded model, was not considered in the control model in order to have comparable models. Only the dependency on microzooplankton and passive ambush omnivore was explored because they represent a link between microbial food web and the classical herbivore food web. In particular, this approach allowed us to investigate the integration of the carbon of microbial origin into the classical phytoplankton – mesozooplankton – higher trophic food web. Dependency was calculated from each of the 50,000 flow solutions by the R package NetIndices (Kones et al., 2009). As contribution and dependency and diet contribution were calculated for each iteration (50,000), a Cliff 's delta analysis could be performed on them in order to define the magnitude of the difference observed (negligible, small, medium or large) between the control and each altered model. This non-parametric effect size measure was performed using the R-cran effsize package 0.8.1

Finally, we described the changes in the nature of ecological pairwise relationships that consider both direct and indirect effects that functional groups exert on one another (Higashi and Patten, 1986; Higashi and Patten, 1989). Four relationships exist: altruism characterizes a relationship beneficial for the source to the detriment of the sink compartment (-,+); competition is harmful for both source and sink (-,-); mutualism provide advantages to both players (+,+); and predation is only beneficial for the sink (+,-). We performed the so called "utility analysis" on the mean values of the flows using the R enaR package version 3.0.0 (Borrett and Lau, 2014).

Results

ENA indices space
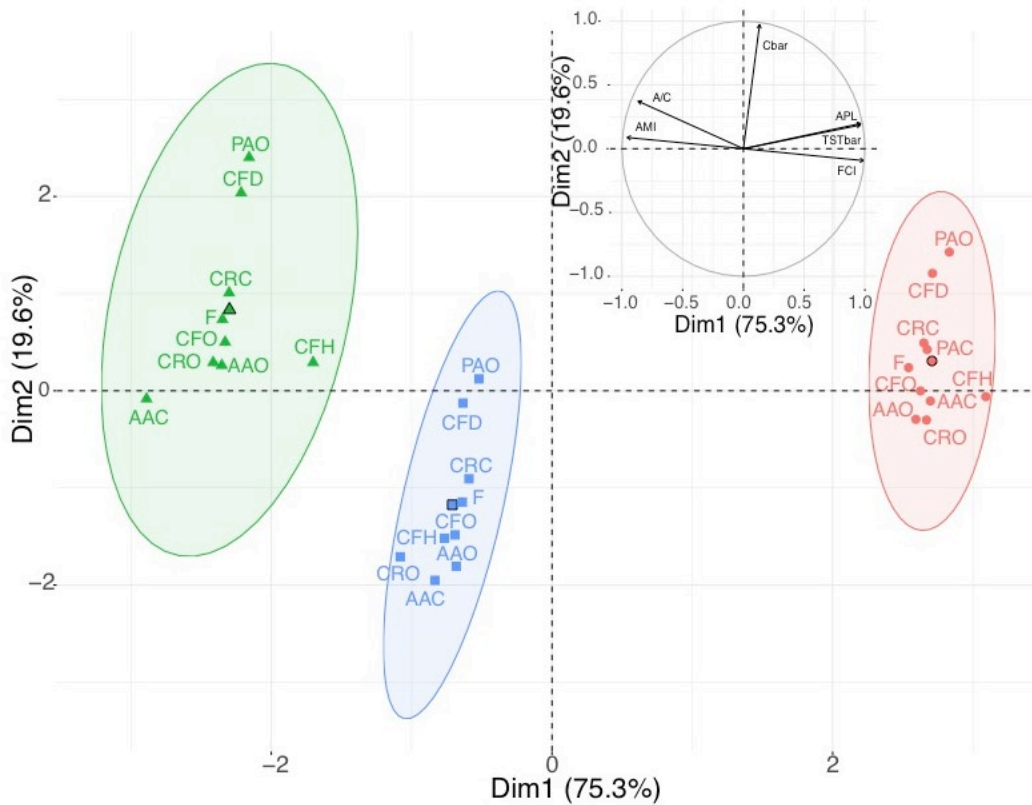
Figure 2. PCA on the mean value of ENA indices for the 28 models. Each ecosystem is represented by a colour: red for the Amundsen Gulf, green and blue for the eastern and western Baffin Bay, respectively. F represents the control (full) model, whereas altered models were named according to the mesozooplankton functional group removed: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for carnivore. TSTbar is the mean compartment activity, APL is the Average Path Length, FCI refers the Finn Cycling index, Cbar means compartmentalization, AMI corresponds to the Average Mutual Information and A/C is the relative Ascendency.

Table 1: Contribution of each variable to PCA axes (in %), presented in decreasing order of contribution to axis 1.

	Axis 1	Axis 2

FCI	21.654	0.741
APL	20.605	3.324
AMI	20.247	0.660
TSTbar	20.493	2.927
A/C	16.605	11.790
Cbar	0.393	80.555

A comprehensive picture emerges from the multivariate analysis of the ENA indices computed from the ensemble of models ran for each regional control and degraded models. The PCA axes 1 and 2 explained, respectively, about 76 % and 19.5% of the variability in ENA indices. Cycling (FCI), carbon retention (APL) and mean compartment activity (TSTbar) were maximized on the right-hand side of the first axis, whereas pathways specialization (AMI) and organization level (A/C) were maximized in the opposite direction. The contribution of each variable to the first axis was almost the same and equal to 20%, except for A/C that contributed to 16.5 % (Table 1). The second axis supported only one variable, the Cbar index that define the existence/strength of sub-systems and contributed to it for 81% (Table 1).

The three ecosystems appeared clearly distinct on the first axis. The Amundsen Gulf, on the right side, presented the highest carbon retention, recycling and mean compartment activity whereas its pathways specialization and organization level were the lowest. At the opposite side on axis 1, the eastern Baffin Bay showed the highest pathways specialization and organization level and hence the lowest recycling, retention and mean compartment activity. The western Baffin Bay that was placed towards the origin of axis 1 showed intermediate properties, while remaining closer to the eastern Baffin Bay models. On the second axis, eastern and western Baffin Bay models were organized following a positive gradient of compartmentalization, while Amundsen Gulf models remained at intermediate values.

Within this ENA space, the position of degraded network models remained close to the position of each ecosystem control models and there was no overlap among models from distinct ecosystems. The dispersion of degraded models around the control model was the highest for the eastern Baffin Bay, whereas it was minimal in Amundsen Gulf. In any case, the removal of Passive Ambush Omnivores (PAO) and Current Feeders Detritivores (CFD) led to a similar response. Removing these functional groups led to an upward shift along the second axis for all ecosystems, which can be interpreted as the emergence of sub-systems or the strengthening of existing sub-systems without affecting any other properties of the ecosystem (i.e. same position on the first axis).

The removal of Active Ambush Carnivores (AAC) and Current Feeder herbivores (CFH) affected differently the three ecosystems. Removing the CFH led to a slight increase in axis 1 coordinates for the Amundsen Gulf and the eastern Baffin Bay ecosystems. In both cases, CFH represented the rightmost point in each region. The removal of CFH reduced pathways specialization and organization level, while increasing cycling, retention and mean activity per compartment. The response of the western Baffin Bay network to the removing of CFH was almost unnoticeable along axis 1. The removal of AAC caused a decrease in axis 1 coordinates in both the eastern and western Baffin Bay ecosystems, whereas it was almost inconsequential for the Amundsen Gulf. Meanwhile, this compartment removal led to a clear decrease in axis 2 coordinates in all ecosystems, revealing the largest decrease in compartmentalization for the eastern and western Baffin Bay. Detailed ENA values associated to Delta Cliff results are presented in figure S2, S3 and S4.

Direct trophic relationships

The diet of each compartment allowed us to track the origin of the carbon directly ingested. The effect of a functional group removal on the carbon circulation was revealed by comparing its impacts on the diets of i) the primary consumers and omnivores (Fig. 3), ii) carnivores (Fig. 4), and iii) the carbon ending up as detritus (Fig. 5). First, the removal of the functional groups deeply affected the diet of primary consumers in both the eastern and western Baffin Bay ecosystems (many orange and red boxes in Fig. 3). For Amundsen Gulf, we observed only small differences in the diet of current feeding herbivore (CFH) when current feeding omnivore (CFO), cruising omnivore (CRO) or passive ambush omnivore (PAO) were removed. The proportion of microzooplankton consumed by CFO was altered in the case of CFH and active ambush carnivore (AAC) removal, whereas the bacterivory by PAO decreased and the consumption of active ambush omnivore (AAO) by CRO increased when CFH and AAC were removed, respectively. In the eastern Baffin Bay, the removal of AAC and CHF altered diet of some particular sink whereas in the western Baffin Bay it was the removal of CFH and CRO that affected diets. In the case of CFH removal, microzooplankton (MIC) fed in higher proportion on phytoplankton in both Baffin Bay ecosystems. To a lesser extent PAO, CFO in the eastern Baffin Bay, joined by CRO in the western Baffin Bay increased their consumption of phytoplankton. This was associated with a significant decrease in consumption of bacteria and detritus (Fig. 3) by PAO and MIC (note that this decrease was lower in WBB). Moreover, microzooplankton was more transferred to its omnivorous predators, which was particularly clear in the eastern Baffin Bay food web. In the latter, the AAC removal decreased herbivory by microzooplankton and its predation by omnivores, whereas it increased microzooplankton bacterivory. When CRO was removed from the western Baffin Bay model, the diet of PAO was the most impacted with an increase in contribution of phytoplankton associated to a decrease in the contribution of all other sources.
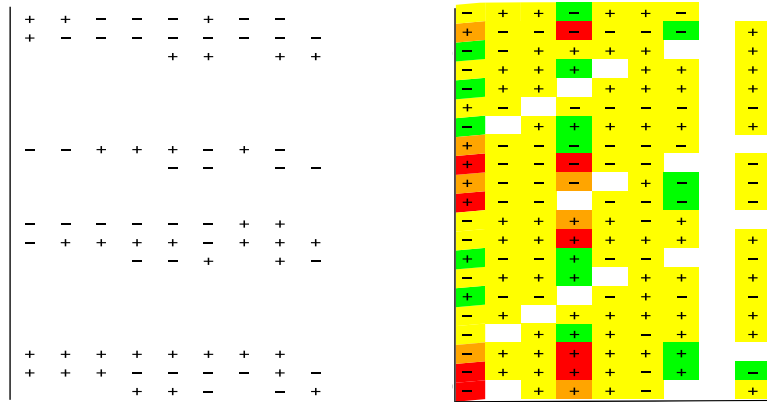
Figure 3. Difference (Cliff's Delta) in the contribution of each source to the consumption of primary consumers/omnivores (sink) for Amundsen Gulf, Eastern and Western Baffin Bay. Test performed on the 50,000 solutions for each flow computed by the LIM. Colour refers to the magnitude of difference according to the following thresholds: yellow = not significant (CD estimate <0.147), green = small difference (CD estimate <0.33), orange = medium difference (CD estimate <0.474), red = large difference (CD estimate >0.474). The difference is computed between the control model and the altered model: + (-) means lower (higher) values for the altered. The functional group removed is indicated on abscissa. The name of the mesozooplankton functional groups was coded as follow: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for carnivore. Other functional groups are PPR: primary producers, MIC: microzooplankton, DET: particulate detritus, BSL: arctic cod larvae. The flows in the rows are ordered as source -> sink.

These changes at lower trophic levels led to changes in the carnivores' diet (Fig. 4). Only the diet of AAC seemed deeply affected by CFH and CRO removal in both Baffin Bay food webs. AAC compensated the loss of CFH by a higher consumption on microzooplankton and CRO in the western Baffin Bay, whereas consumption on all its preys was altered in the eastern Baffin Bay food web. The loss of CRO caused opposite difference with the alteration of all prey contribution

(except CRO) to the AAC diet in the western Baffin Bay, while only consumption on microzooplankton, CFH and AAO was altered in the eastern Baffin Bay. On the contrary, although small changes were observed in the primary consumers/omnivores diet, those of carnivores were clearly altered in the Amundsen Gulf. It was mainly the diet of AAC that was modified with an increase in the contribution of CFO and CRO. The removal of CRO caused an increase in the contribution of CFH and CFO to the diet of AAC and only the consumption of CFH by AAC was altered in the removal of CFO. The diet of BSL remained unchanged whatever the functional group removed.

Figure 4. Difference (Cliff's Delta, CD) in the contribution of each source to the consumption of carnivores (sink) for Amundsen Gulf, Eastern and Western Baffin Bay. Test performed on the 50,000 solutions for each flow computed by the LIM. Colour refers to the magnitude of difference according to the following thresholds: yellow = not significant (CD estimate *<0.147),* green = small difference (CD estimate <0.33), orange = medium difference (CD estimate *<0.474),* red = large difference (CD estimate >0.474). The difference is computed between the control model and the altered model: + (-) means lower (higher) values for the altered. The functional group removed is indicated on abscissa. The name of the mesozooplankton functional groups was coded as follow: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for

carnivore. Other functional groups are MIC: microzooplankton, BSL: arctic cod larvae. The flows in the rows are ordered as source -> sink.

Finally, the source of detritus was affected in the case of AAC, CFH or CRO removal in both Baffin Bay ecosystems. CFH loss caused an increase in the contribution of microzooplankton and PAO to the two detritus in these ecosystems (Fig. 5). Phytoplankton contributed more to dissolved detritus whereas CRO contributed to particulate detritus when CFH was removed. AAC loss led to a large increase in the contribution of phytoplankton to dissolved carbon while CRC, CRO, CFH and BSL increased their contribution to particulate detritus, in the eastern Baffin Bay food web. On the contrary microzooplankton, bacteria and CFD reduced their contribution to detritus. The consequences of functional group removal were different in the Amundsen Gulf ecosystem. For CFH and CRO removal an increase in the contribution of CFO to both detritus associated to an increased proportion of phytoplankton flowing to detritus was noted. More phytoplankton and PAO carbon flowed to dissolved carbon when CFH was lost whereas more bacteria carbon was received by detritus for PAO removal.
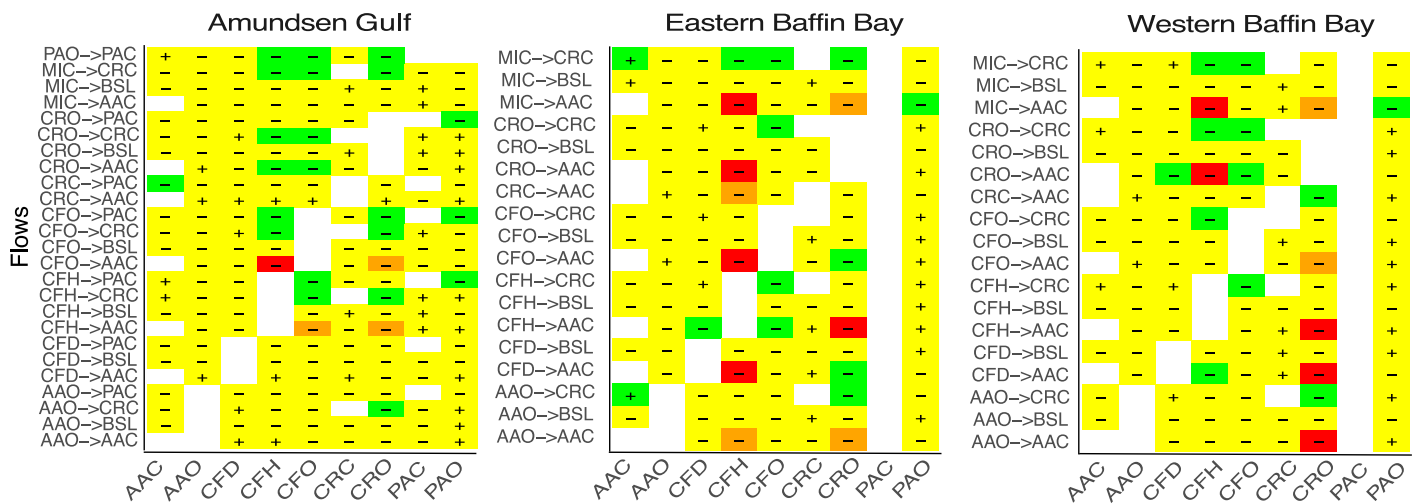
Figure 5. Difference (Cliff's Delta) in the contribution of each source to the detritus compartments (sink) for Amundsen Gulf, Eastern and Western Baffin Bay. Test performed on the 50,000 solutions for each flow computed by the LIM. Colour refers to the magnitude of difference according to the following thresholds: yellow = not significant (CD estimate <*0.147),* green = small difference (CD estimate <0.33), orange = medium difference (CD estimate <*0.474)*, red = large difference (CD estimate >0.474). The difference is computed between the control model and the altered model: + (-) means lower (higher) values for the altered. The functional group removed is indicated on abscissa. The name of the mesozooplankton functional groups was coded as follow: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for carnivore. Other functional groups are PPR: primary producers, MIC: microzooplankton, DET: particulate detritus, DOC: dissolved organic carbon; BSL: arctic cod larvae. The flows in the rows are ordered as source -> sink.

Dependency: direct and indirect pathways

The dependency informs on the quality of the circulation of carbon from a particular source. Here we focused on transfer of the carbon of microbial origin, which enters into the grazing chain via the microzooplankton and the omnivorous passive ambush feeders (PAO). A clear increase in dependency on microzooplankton was observed when CFH and CRO were removed in the eastern Baffin Bay, while AAC removal lowered dependency on microzooplankton. In the western Baffin Bay, only CFH removal largely increased the dependency on microzooplankton. In the Amundsen Gulf ecosystem, the dependency of microzooplankton was not altered (Fig. 6 A), whereas a small increase in the dependency on PAO was observed for the removal of CHF, CRO and CFO (Fig. 6 B). A clear increase in the dependency of PAO was the result of the CHF as well as CRO in the western Baffin Bay ecosystem, whereas only CFH removal caused a large increase in PAO dependency in the eastern Baffin Bay ecosystem.
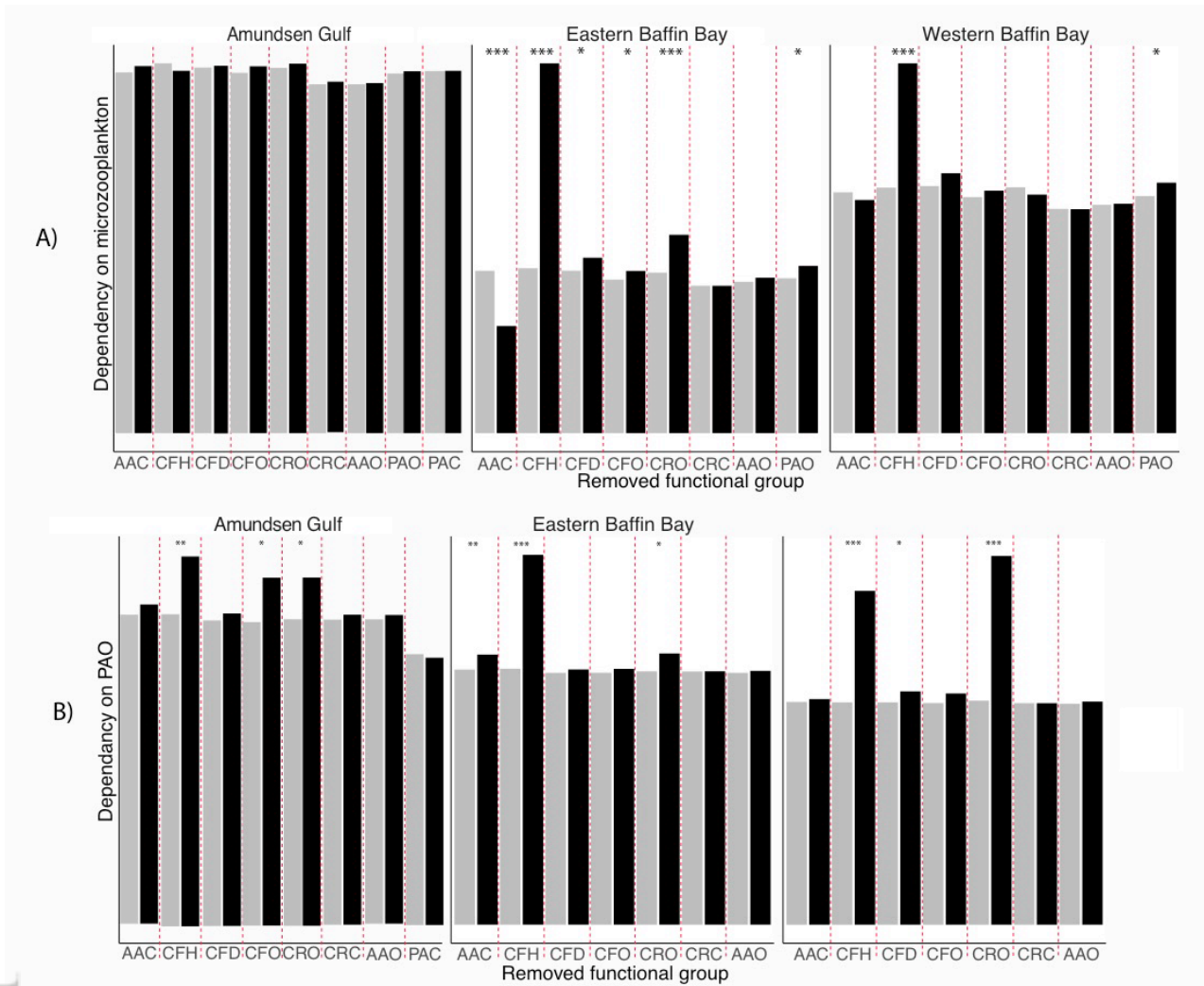
Figure 6. Dependency on microzooplankton (A) and on passive ambush omnivore (PAO; B) of sinks in the food webs for Amundsen Gulf, eastern Baffin Bay and western Baffin Bay. Light grey: dependency in control models, where the functional group removed in the degraded model was not considered as sink in order to have comparable models. Black: dependency in altered models, identified by the functional group removed. The name of the mesozooplankton functional groups was coded as follow: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for carnivore. Dependency analysis was performed on the 50,000 solutions of each flow, with a non-parametric effect size measure, Cliff's delta (CD): *** =

large difference (CD estimate >0.474); ** = medium difference (CD estimate *<0.474)*; * small difference (CD estimate <0.33).
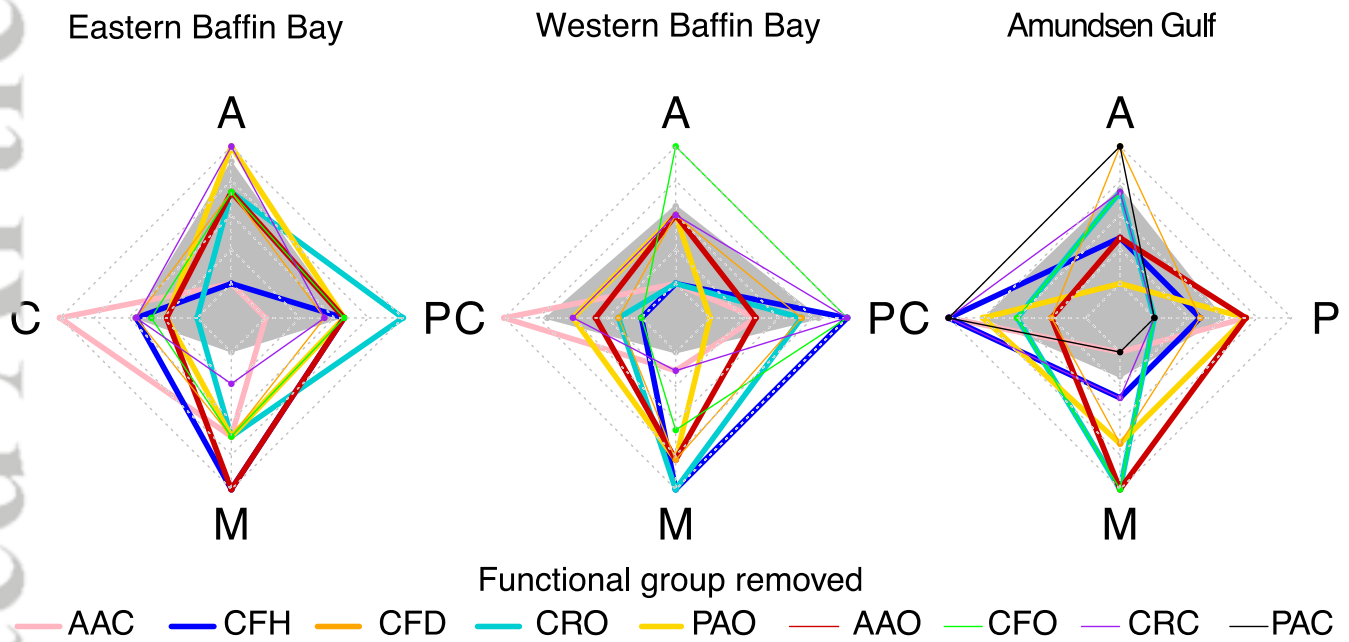
Pairwise interactions

Figure 7: Proportion of each type of pairwise interaction (source, sink). A: altruism (+,-); P: predation(-,+); M: mutualism(+,+); C: competition (-,-) in the three distinct ecosystems: Amundsen Gulf, eastern Baffin Bay and western Baffin Bay. Coloured lines represent the compartment removed in each run. The grey area corresponds to the space defined by values from the control model with all functional groups. The minimal and maximal values observed for each type of relationship in all runs, including the control model, were used to draw the radar chart. The minimal values are in the centre of the radar plot, while the maximum values were at the edge. Dots placed far from the grey surface present a strong difference from the control. The name of the mesozooplankton functional groups was coded as follow: i) the first two letters correspond to feeding strategies with AA and PA for active and passive ambush, respectively, CF for current feeder, and CR for cruiser; ii) the last letter refers to the type of prey with H for herbivore, D for detritivore, O for omnivore and C for carnivore.

The detailed consequences of the removal of a particular compartment on the pairwise relationships varied according to the ecosystem considered (Fig. 7). In eastern Baffin Bay, only altruism decreased after CFH removal to the benefit of mutualism, while competition remained the same. In western Baffin Bay, competition decreased in response to CFH removal, whereas it increased in the Amundsen Gulf. The removal of carnivorous groups (AAC, CRC and PAC) caused an increase in the competition in the Amundsen Gulf, while in the Baffin Bay ecosystems only AAC removal enhanced competition.

Discussion

This study revealed the role of different mesozooplankton functional groups in the functioning of three Arctic marine ecosystems. The removal of cruiser carnivores (CRC) and active ambush omnivores (AAO) did not lead to a clear response of any of the food webs (except for some changes in the nature of pairwise relationships), likely due to their low involvement in the carbon transfer (< 1 % of the total feeding flows, Fig. S1). The loss of passive ambush omnivores (PAO) and current feeders detritivores (CFD) led to common alteration of connectivity between compartments in all ecosystems (increase in the compartmentalization Fig. 2). As both feed on components of the microbial loop (detritus and bacteria essentially), they insure connectivity between the microbial and grazing food chains. This connectivity was directly altered by their removal.

The functional groups current feeding herbivores (CFH), active ambush carnivores (AAC), current feeding omnivores (CFO), cruising omnivores (CRO) clearly altered the carbon circulation within all food webs. However, the effects of a functional group's removal on both carbon circulation and the resulting ecosystem functioning were specific to each ecosystem.

Current feeding herbivore (CFH)

CFH was composed of the three dominant congeneric *Calanus* copepod species (The Arctic *Calanus glacialis* and *C. hyperboreus*, and the boreal expatriate *C. finmarchicus*) in the Baffin Bay ecosystems while *C. finmarchicus* was not present in the Amundsen Gulf. This functional group was the main grazer of primary production during the phytoplankton bloom period (Darnis et al., 2012; Falk-Petersen et al., 2009) having the most influence in carbon transfer in each ecosystem (Fig. S1). Its loss caused a complete reorganization of the carbon circulation in both Baffin Bay ecosystems. The removal of CFH allowed other grazers, especially microzooplankton and passive ambush omnivore (PAO), to feed on the limited phytoplankton resources. In turn, the higher consumption on microzooplankton and PAO by predators (higher dependencies in fig. 6) insured a better connectivity between the microbial loop and the "grazing food web" linking phytoplankton to mesozooplankton. On the contrary, the removal of CFH did not deeply alter the carbon circulation within the Amundsen Gulf food web (Fig. 3). Although its primary production was similar to both Baffin Bay ecosystems, the higher bacterial production and bacterivory (Fig. S6) satisfied the PAO and microzooplankton needs (Fig. S6). The distinct consequences on the whole network properties highlighted specific role of CFH in each ecosystem. As the removal of CFH reduced the specialization of pathways (reduction in AMI, Fig S2 and S3) in the Amundsen Gulf and in the eastern Baffin Bay, CFH appeared as the main driver of carbon circulation. Since the carbon recycling was largely impacted (FCI in Fig S3) in the western Baffin Bay, the crucial role of CFH in recycling was highlighted. This is linked to its capacity to produce dissolved organic matter and faecal pellets (Møller et al., 2003; Tang et al., 2010) supporting bacterial production and coprophagy (Steinberg and Landry, 2017).

The distinct impact of the CFH removal on the pairwise relationships shaded a new light on the role of CFH in the western Baffin Bay and the Amundsen Gulf ecosystems. The decrease in competition (-,-) in the western Baffin Bay revealed that CFH seems to be the *source* of competition among functional groups, whereas its increase in the Amundsen Gulf suggested that CFH is involved the *regulation* of competition between functional groups. This can be explained by the distinct kind of competition occurring in the Amundsen Gulf versus the western Baffin Bay ecosystems. In the western Baffin Bay ecosystem, the competition is an exploitative competition involving several consumers feeding on the same resources, like phytoplankton (Wootton, 1994), while it seems to be an apparent competition due to various preys that are consumed by a common predator (Wootton, 1994) in the Amundsen Gulf.

Active Ambush Carnivores (AAC)

Contrary to CFH, AAC is a predator located at the highest trophic level in these models. In the three control models, this functional group mainly feeds on motile preys, like microzooplankton, CFH and cruiser omnivore (CRO) (Almeda et al., 2018). Its members can also feed on all others active feeder functional groups from the mesozooplankton (Djeghri et al., 2018). Since AAC was the main predator feeding on most living compartments, its role could not be "replaced" by any other and its removal led to a surplus of secondary production that needed to be exported from the system to satisfy the trophic networks balance. This was shown by a common decrease in carbon retention and in the total carbon contained within the system in the three ecosystems (APL and T.., respectively in Fig. S2-S3-S4).

The increased competition after the loss of a predator in all three ecosystems is a common occurrence in ecosystems (e.g. Donohue et al., 2017). The further consequences of AAC removal

was linked to the role of CFH in each ecosystem. In Baffin Bay ecosystems, AAC removal affected the distribution of primary production to both CFH and microzooplankton, with consequences on their respective predation by higher consumers. In the eastern Baffin Bay, the primary production supported CFH consumption and its transfer to the higher trophic levels to the detriment of microzooplankton (fall in dependency Fig. 6A), while in the western Baffin Bay the higher carbon flowing through the system sustained CFH and microzooplankton consumption without affecting their predation by higher trophic levels (dependency on microzooplankton unaltered Fig 6A). Moreover, AAC appeared to stimulate carbon recycling in both ecosystems. On the contrary, in the Amundsen Gulf the removal of AAC affected predation of higher consumers. The removal of the main predator, AAC, made possible the predation of its preys (especially microzooplankton and AAO) by other predators (CFO and CRO). As a consequence, the competition between predators for a common prey increased. The associated decrease in flow specialization (decrease in AMI Fig. S2) proved that carbon circulation was less constrained, i.e. controlled in part by AAC.

The cruiser omnivores (CRO) and current feeder omnivores (CFO)

The removal of CRO and CFO decreased the quantity of carbon flowing through the system and the carbon retention but enhanced the organisation of flows in the Amundsen Gulf, whereas in the Baffin Bay ecosystems only CRO altered these properties. This could be explained by the relative contribution of CFO and CRO to the diet of various compartments. As CRO and CFO present an active feeding mode, similar to the CFH functional group that is known to enhance predation on this group compared to ambush feeders (Almeda et al., 2017; van Someren Gréve et al., 2017), these three functional groups contributed in similar proportion to the diet of compartments in the

Amundsen Gulf (Fig S6). On the contrary, the contribution is skewed in favour of CFH and CRO consumption and in favour of CFH in western and eastern Baffin Bay, respectively (Fig S6). The greater involvement in internal flows (Fig S1) of CRO in western Baffin Bay and of CRO and CFO in the Amundsen Gulf caused a reorganisation of carbon flows via a higher detrital contribution of the less generalist PAO (increase in PAO dependency, Fig 6B) when they are removed. The consequences of removal of CFO and CRO were similar in the Amundsen Gulf, which suggested a functional redundancy of these two functional groups. When either one of these groups was removed, the remaining one seemed to ensure the vacant function. Such an apparent functional redundancy is known to favour ecosystem resilience and resistance in the case of perturbation (e.g.(Wardle et al., 2000).

Insight into ecosystems functioning

Although, in general, the same functional groups caused similar responses in all three ecosystems, there were some clear regional differences. Both Baffin Bay ecosystems tended to react more similarly than the Amundsen Gulf ecosystem. We offer two hypotheses, non-mutually exclusive: 1) a methodological cause and 2) an ecological origin.

First, the data used to build the three full trophic network models (controls) could explain some of the observed difference. On one hand, both the eastern and western Baffin Bay models integrated similar data on net primary production, bacterial production, mesozooplankton biomasses, etc. (see details in Saint-Béat et al., 2020) obtained during the 2016 GreenEdge campaign (Massicotte et al., 2020). On the other hand, the Amundsen Gulf model was based on a dataset that containing more information on flows (Table S1), obtained during the 2008 Circumpolar Flaw Lead System Study (Forest et al., 2011; Nguyen et al., 2012). Herbivory by copepod species making the bulk of

mesozooplankton biomass (*Calanus* spp. and *Metridia longa,* grouped in the CFH and CRO functional groups, respectively) and microzooplankton bacterivory (Vaqué et al., 2008) were experimentally estimated. As a result, the linear inverse model algorithm applied to the Amundsen Gulf trophic network had to obey more constraints limiting the development of compensatory mechanisms following functional groups removal. This could partially explain the lower variability of the responses to functional groups removal obtained for the Amundsen Gulf ecosystem.

Second, the variability of each ecosystem response can be partially explained by the intrinsic ecological properties of the control model. Indeed, the ecological properties of the food web appeared determinant for its stability property (i.e. its ability to maintain its current state) when facing a perturbation (e.g. Lawrence et al., 2012; Saint-Béat et al., 2015; Suttle et al., 2007). Ecology recognizes two types of flows (Ulanowicz, 1997) : 1) *direct* pathways linking a prey to its predator that bring efficiency to the trophic network, and 2) *redundant* pathways linking indirectly a prey to its predator (via one or several intermediates) that bring flexibility to the trophic network. The relative Ascendency (A/C) that measures the trade-off between efficiency and flexibility, appears as the best metric to predict ecosystem stability (Canning and Death, 2018). The first PCA axis revealed that for all scenarios of functional groups removal, the eastern Baffin Bay ecosystem presented the highest relative Ascendency and thus the highest efficiency, whereas the Amundsen Gulf ecosystem was the most redundant. As a result, it seems that the structure of the Amundsen Gulf food web was able to limit the impacts of a functional group loss on its ecological properties, thanks to its highest proportion of redundant pathways allowing a predator to feed on alternative preys without deeply disrupting carbon circulation. On the contrary, in the more ascendant eastern Baffin Bay ecosystem, alternate pathways were limited, and the removal of some functional groups led to the significant alteration of ecosystem functioning.

However, the closer relative Ascendency values between the western Baffin Bay and the Amundsen Gulf ecosystems suggest that factors other than the food web ecological properties could explain the distinct responses of both ecosystems to the removal of some functional groups. The actual amount of resources available also plays a central role in the stability of an ecosystem facing perturbations in its trophic network (Stachowicz et al., 2007). When most of the available resources is already circulating among the food web compartments, this limits the possibilities of reorganization of the trophic network after the removal of one group. Moreover, the number of compartments involved in the transfer of carbon from the producers to the top consumers (efficiency) is a strong determinant of how diversity loss affects ecosystem functioning (Duffy et al., 2005). As a result, we hypothesize that the higher resources availability (high T..) combined with a more efficient use of carbon (i.e. higher APL) could limit the consequences of the loss of any functional group on the functioning of the Amundsen Gulf ecosystem. We think that more comparative studies between contrasted ecosystems (or ecosystem states) and experimental modifications of the quantity and availability of resources in plankton ecosystems could help to test this hypothesis.

Functional groups and climate change

While this study was not designed to analyze consequences of climate change on Arctic marine ecosystem functioning, it points at a distinct response of Arctic marine ecosystems to changes in functional traits assemblage that are forecasted for this ocean (Benedetti et al., 2021). The profound and rapid alteration of sea ice extent (Kwok et al., 2009) and biogeochemical conditions (Polyakov et al., 2020) that have been observed for the past decade in the Arctic Ocean have already deeply transformed its biological environment, at various trophic levels (e.g., (Ardyna and

Arrigo, 2020; Grebmeier, 2012). The most striking impact has been a decrease of the planktonic organisms' size observed in both phytoplankton (Li et al., 2009) and zooplankton (Benedetti et al., 2021). Since the size of an organism is a master trait that controls most of its biological functions, and in particular its trophic interactions, such changes will profoundly affect food webs throughout the Arctic Ocean (Kortsch et al., 2015). However, the exact nature of the eventual consequences on carbon circulation within food webs and on ecosystems' functioning and services remain elusive. The approach developed in this study paves the way to a more thorough investigation of this issue. Coupling experimental and modelling approaches to study changing functional traits composition in planktonic ecosystems is a powerful way to identify and quantify unexpected changes occurring via indirect, complex pathways linking several levels of organisation. Although this kind of study does not intend to predict future ecosystem functioning, it offers explanations and testable hypotheses regarding complex ecosystems responses to environmental perturbations.

Conclusion

The functioning of three marine Arctic ecosystems was affected the most by the current feeding herbivores (CFH) and the active ambush carnivores (AAC) functional groups. However, the removal of either the CFH or AAC did not lead to a unique response in ecosystem functioning. Depending on the marine ecosystem considered, it led to subtle differences on the trophic networks' complexity (presence of sub-cycles) and stability (ability to cope with perturbations) properties. The removal of several other functional groups did not affect ecosystem functioning as much, likely due to their relatively low respective activity within the ecosystem considered. Our results revealed that the ecological properties and productivity of the network formed by these functional groups significantly modulate their role and the magnitude of the impact of their

removal on the ecosystem functioning. The presence or absence of a specific functional group does not seem to be associated with a unique and predictable set of ecosystem properties. Forecasting changes in the functioning of marine ecosystems in response to the rapidly increasing impacts of climate change and anthropic pressure requires a more detailed knowledge of the trophic network, such as its productivity and its carbon circulation properties.

Bibliography

Almeda R, van Someren Gréve H, Kiørboe T. 2017. Behavior is a major determinant of predation risk in zooplankton. *Ecosphere* **8**(2): e01668.

Almeda R, van Someren Gréve H, Kiørboe T. 2018. Prey perception mechanism determines maximum clearance rates of planktonic copepods. *Limnology and Oceanography* **63**(6): 2695-2707.

AMAP. 2019. Arctic Climate Change Update 2019: An update to key findings of Snow, Water, Ice, and Permafrost in the Arctic (SWIPA) 2017.: 12 pp. Available at https://www.amap.no/documents/doc/amap-climate-change-update-2019/1761.

Ardyna M, Arrigo KR. 2020. Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change* **10**(10): 892-903.

Arrigo KR, van Dijken GL. 2015. Continued increases in Arctic Ocean primary production. *Progress in Oceanography* **136**: 60-70.

Bélanger S, Babin M, Tremblay J-É. 2013. Increasing cloudiness in Arctic damps the increase in phytoplankton primary production due to sea ice receding. *Biogeosciences* **10**(6): 4087-4101.

Benedetti F, Vogt M, Elizondo UH, Righetti D, Zimmermann NE, et al. 2021. Major restructuring of marine plankton assemblages under global warming. *Nature communications* **12**(1): 1-15.

Benedetti F, Vogt M, Righetti D, Guilhaumon F, Ayata SD. 2018. Do functional groups of planktonic copepods differ in their ecological niches? *Journal of Biogeography* **45**(3): 604-616.

Blais M, Ardyna M, Gosselin M, Dumont D, Bélanger S, et al. 2017. Contrasting interannual changes in phytoplankton productivity and community structure in the coastal Canadian Arctic Ocean. *Limnology and Oceanography* **62**(6): 2480-2497.

Borrett SR, Lau MK. 2014. enaR: an R package for ecosystem network analysis. *Methods in Ecology and Evolution* **5**(11): 1206-1213.

Boyd PW, Claustre H, Levy M, Siegel DA, Weber T. 2019. Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* **568**(7752): 327-335.

Darnis G, Robert D, Pomerleau C, Link H, Archambault P, et al. 2012. Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. *Climatic Change* **115**(1): 179-205. doi:10.1007/s10584-012-0483-8.

Djeghri N, Atkinson A, Fileman ES, Harmer RA, Widdicombe CE, et al. 2018. High prey-predator size ratios and unselective feeding in copepods: A seasonal comparison of five species with contrasting feeding modes. *Progress in Oceanography* **165**: 63-74.

Donohue I, Petchey OL, Kéfi S, Génin A, Jackson AL, et al. 2017. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. *Global Change Biology* **23**(8): 2962-2972.

Duffy E, J, Richardson P, J, Kristin F E. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* **8**(3): 301-309.

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR. 2009. Lipids and life strategy of Arctic Calanus. *Marine Biology Research* **5**(1): 18-39. doi:10.1080/17451000802512267.

Fath BD, Patten BC. 1998. Network synergism: emergence of positive relations in ecological systems. *Ecological Modelling* **107**(2-3): 127-143.

Forest A, Galindo V, Darnis G, Pineault S, Lalande C, et al. 2011. Carbon biomass, elemental ratios (C:N) and stable isotopic composition (13C, 15N) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). *Journal of Plankton Research* **33**(1): 161-178. doi:10.1093/plankt/fbq103.

Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov AV, et al. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences* **114**(46): 12202-12207. doi:doi:10.1073/pnas.1706080114.

Grebmeier JM. 2012. Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. *Annual Review of Marine Science* **4**(1): 63-78. doi:10.1146/annurev-marine-120710-100926.

Higashi M, Patten BC. 1986. Further aspects of the analysis of indirect effects in ecosystems. *Ecological modelling* **31**(1-4): 69-77.

Higashi M, Patten BC. 1989. Dominance of indirect causality in ecosystems. *The American Naturalist* **133**(2): 288-302.

Kay JJ, Graham LA, Ulanowicz RE. 1989. A detailed guide to network analysis. *Network analysis in marine ecology*. Springer: 15-61.

Kiørboe T. 2011. How zooplankton feed: mechanisms, traits and trade‐offs. *Biological reviews* **86**(2): 311-339.

Kiørboe T, Visser A, Andersen KH. 2018. A trait-based approach to ocean ecology. *ICES Journal of Marine Science* **75**(6): 1849-1863.

Kones JK, Soetaert K, van Oevelen D, Owino JO. 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. *Ecological Modelling* **220**(3): 370-382. doi:10.1016/j.ecolmodel.2008.10.012.

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M. 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences* **282**(1814): 20151546. doi:doi:10.1098/rspb.2015.1546.

Kwok R, Cunningham G, Wensnahan M, Rigor I, Zwally H, et al. 2009. Thinning and volume loss of the Arctic Ocean sea ice cover: 2003–2008. *Journal of Geophysical Research: Oceans* **114**(C7).

Latham LG. 2006. Network flow analysis algorithms. *Ecological Modelling* **192**(3-4): 586-600. doi:10.1016/j.ecolmodel.2005.07.029.

Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, et al. 2012. Species interactions alter evolutionary responses to a novel environment. *PLoS biology* **10**(5): e1001330.

Lê S, Josse J, Husson F. 2008. FactoMineR: an R package for multivariate analysis. *Journal of statistical software* **25**(1): 1-18.

Li WK, McLaughlin FA, Lovejoy C, Carmack EC. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* **326**(5952): 539-539.

Martini S, Larras F, Boyé A, Faure E, Aberle N, et al. 2021. Functional trait‐based approaches as a common framework for aquatic ecologists. *Limnology and Oceanography* **66**(3): 965-994.

Massicotte P, Amiraux R, Amyot M-P, Archambault P, Ardyna M, et al. 2020. Green Edge ice camp campaigns: understanding the processes controlling the under-ice Arctic phytoplankton spring bloom. *Earth System Science Data* **12**(1): 151-176.

Møller EF, Thor P, Nielsen TG. 2003. Production of DOC by Calanus finmarchicus, C. glacialis and C. hyperboreus through sloppy feeding and leakage from fecal pellets. *Marine Ecology Progress Series* **262**: 185-191.

Moloney CL, Field JG. 1989. General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. *Limnology and Oceanography* **34**(7): 1290-1299. doi:10.4319/lo.1989.34.7.1290.

Mutshinda CM, Finkel ZV, Widdicombe CE, Irwin AJ. 2016. Ecological equivalence of species within phytoplankton functional groups. *Functional Ecology* **30**(10): 1714-1722.

Nguyen D, Maranger R, Tremblay JÉ, Gosselin M. 2012. Respiration and bacterial carbon dynamics in the Amundsen Gulf, western Canadian Arctic. *Journal of Geophysical Research: Oceans* **117**(C9).

Nogues Q, Raoux A, Araignous E, Chaalali A, Hattab T, et al. 2021. Cumulative effects of marine renewable energy and climate change on ecosystem properties: Sensitivity of ecological network analysis. *Ecological Indicators* **121**: 107128.

Polyakov IV, Alkire MB, Bluhm BA, Brown KA, Carmack EC, et al. 2020. Borealization of the Arctic Ocean in Response to Anomalous Advection From Sub-Arctic Seas. *Frontiers in Marine Science* **7**. doi:10.3389/fmars.2020.00491.

Renaud PE, Daase M, Banas NS, Gabrielsen TM, Søreide JE, et al. 2018. Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience. *ICES Journal of Marine Science* **75**(6): 1871-1881.

Saint-Béat B, Baird D, Asmus H, Asmus R, Bacher C, et al. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological indicators* **52**: 458-471.

Saint-Béat B, Fath BD, Aubry C, Colombet J, Dinasquet J, et al. 2020. Contrasting pelagic ecosystem functioning in eastern and western Baffin Bay revealed by trophic network modeling. *Elementa: Science of the Anthropocene* **8**.

Saint-Béat B, Maps F, Babin M. 2018. Unraveling the intricate dynamics of planktonic Arctic marine food webs. A sensitivity analysis of a well-documented food web model. *Progress in Oceanography*.

Schmitz OJ, Leroux SJ. 2020. Food Webs and Ecosystems: Linking Species Interactions to the Carbon Cycle. *Annual Review of Ecology, Evolution, and Systematics* **51**: 271-295.

Stachowicz JJ, Bruno JF, Duffy JE. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. *Annu Rev Ecol Evol Syst* **38**: 739-766.

Steinberg DK, Landry MR. 2017. Zooplankton and the ocean carbon cycle. *Annual Review of Marine Science* **9**: 413-444.

Suttle K, Thomsen MA, Power ME. 2007. Species interactions reverse grassland responses to changing climate. *science* **315**(5812): 640-642.

Szyrmer J, Ulanowicz RE. 1987. Total flows in ecosystems. *Ecological Modelling* **35**(1-2): 123-136.

Tang KW, Turk V, Grossart H-P. 2010. Linkage between crustacean zooplankton and aquatic bacteria. *Aquatic Microbial Ecology* **61**(3): 261-277.

Ulanowicz RE. 1986. *Growth and Development Ecosystems Phenomenology*. toExcel Press.

Ulanowicz RE. 1997. *Ecology, the ascendent perspective: Robert E. Ulanowicz*. Columbia University Press.

Van den Meersche K, Soetaert K, Van Oevelen D. 2009. xsample (): an R function for sampling linear inverse problems. *Journal of Statistical Software* **30**(Code Snippet 1 %@ 1548-7660).

Van Oevelen D, Van den Meersche K, Meysman FJ, Soetaert K, Middelburg JJ, et al. 2010. Quantifying food web flows using linear inverse models. *Ecosystems* **13**(1): 32-45.

van Someren Gréve H, Almeda R, Kiørboe T. 2017. Motile behavior and predation risk in planktonic copepods. *Limnology and Oceanography* **62**(5): 1810-1824.

Vaqué D, Guadayol O, Peters F, Felipe J, Angel-Ripoll L, et al. 2008. Seasonal changes in planktonic bacterivory rates under the ice‐covered coastal Arctic Ocean. *Limnology and Oceanography* **53**(6): 2427-2438.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, et al. 2007. Let the concept of trait be functional! *Oikos* **116**(5): 882-892.

Wardle DA, Bonner KI, Barker GM. 2000. Stability of ecosystem properties in response to above‐ground functional group richness and composition. *Oikos* **89**(1): 11-23.

Wootton JT. 1994. The nature and consequences of indirect effects in ecological communities. *Annual review of ecology and systematics* **25**(1): 443-466.

Supporting Information

Appendix S1: Description of the three Arctic marine ecosystems studied.

Table S1: List of parameters used to constrain the food web LIM models

Table S2: List of species sampled in the three ecosystems.

Table S3: Composition of the nine mesozooplankton functional groups.

Table S4-S6: Abundance (ind.m^{-2}), range of size (μm) and range of biomass (μgC.m^{-2}) of mesozooplankton species found in the three ecosystems.

Figure S1: Involvement of mesozooplankton functional group.

Figure S2-S4: Boxplot presenting the values for ENA indices describing six main ecological properties of the three Arctic marine ecosystems.

Figure S5: Bacterivory on Herbivory ratio observed in the three ecosystems for the control model.

Figure S6: Diet of each consumers and detritus in the three ecosystems for the control model.