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**The phenology of key *Calanus* species  
in the context of food demand of little auk (*Alle alle*)  
nesting on Spitsbergen**

PhD thesis

written under the supervision of  
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**Fenologia kluczowych gatunków z rodzaju *Calanus*  
w kontekście zapotrzebowania pokarmowego alczyka (*Alle alle*)  
gniazdującego na Spitsbergenie**

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## STRESZCZENIE

Arktyka jest miejscem, gdzie zachodzą jedne z najszybszych i najbardziej spektakularnych zmian spowodowanych ocieplaniem klimatu. Wzrost temperatury i natężenia napływu wód pochodzenia atlantyckiego do Arktyki zaburza procesy kształtujące strefy frontalne i układ mas wodnych, przyczyniając się zarówno do lokalnych, jak i wielkoskalowych zmian środowiskowych. Zanik lodu morskiego, wzrost temperatury wody morskiej i zmiany w stratyfikacji istotnie wpływają na rozmiar, strukturę i synchronizację morskiej produkcji biologicznej.

Przewiduje się, że postępujący wzrost temperatury wody morskiej istotnie wpłynie na przekształcanie pelagicznych sieci troficznych, w kierunku zastępowania dużych, zimnolubnych organizmów planktonowych, przez mniejsze gatunki borealne. Znaczne zmiany parametrów środowiskowych wpłyną także na redukcję rozmiarów ciała organizmów w obrębie gatunku. Do niedawna przewidywano, że zmiany te będą miały negatywne konsekwencje dla drapieżników szczytowych, jednak przewiduje się, że transfer energii do wyższych poziomów troficznych może okazać się bardziej wydajny niż wcześniej zakładano. Niestety taki optymistyczny scenariusz może nie dotyczyć ściśle wyspecjalizowanych planktonożernych ptaków morskich, selektywnie odławiających głównie duże, wysokokaloryczne widłonogi z rodzaju *Calanus*.

W kontekście dynamicznych zmian zachodzących w morskim środowisku arktycznym istotne jest monitorowanie ich wpływu na organizmy morskie, a w szczególności widłonogi z rodzaju *Calanus*, które ze względu na swoją wysoką wartość energetyczną, należą do kluczowych gatunków w pelagicznych ekosystemach Arktyki. W Oceanie Arktycznym dominują trzy gatunki z rodzaju *Calanus*: *C. glacialis*, *C. finmarchicus* i *C. hyperboreus*. W pracy skupiono się na dwóch pierwszych, bliźniaczych gatunkach, ponieważ dominują one w wodach Svalbardu oraz w diecie alczyka. Z kolei *C. hyperboreus* jest gatunkiem głębokowodnym, bardzo rzadko łowionym przy użyciu standardowych sieci planktonowych, sporadycznie występującym w diecie alczyków gniazdujących na Spitsbergenie.

Kluczowa rola *Calanus* spp. w sieci troficznej opiera się na transferze kwasów tłuszczowych omega-3, które są niezbędne w procesach wzrostu i reprodukcji wszystkich organizmów morskich. Nawet 60% objętości ciała tych widłonogów wypełnione jest tłuszczami magazynowanymi w tzw. worku tłuszczowym. Do niedawna sugerowano, że

ilość lipidów w organizmie jest cechą gatunkową i wyższą ich zawartość przypisywano zwykle większemu, arktycznemu *C. glacialis*, w porównaniu z mniejszym, więc potencjalnie mniej energetycznie wartościowym, borealnym *C. finmarchicus*. Podejście to podkreślało odmienną rolę obu gatunków w ekosystemie arktycznym. Jednak najnowsze badania wykazały, że zawartość lipidów zależy w dużej mierze od wielkości ciała. Najprawdopodobniej dotychczasowy sposób postrzegania tego problemu wynikał z błędnej identyfikacji obu gatunków, gdyż morfologicznie bardzo do siebie podobne *C. glacialis* i *C. finmarchicus*, do tej pory były rozróżniane głównie na podstawie różnic w długości ciała (prosomy). Techniki molekularne stosowane w ostatnich badaniach wykazały, że zakresy wielkości tych dwóch gatunków w dużej mierze się pokrywają i są znacznie szersze niż wcześniej zakładano. Dlatego, ze względu na dowiedzioną podobną funkcję obu gatunków i trudności z ich właściwym rozróżnieniem, dla celów tej pracy *C. glacialis* i *C. finmarchicus* zostały sklasyfikowane jako jedno grupa *Calanus* spp.

W zależności od odmiennych warunków środowiskowych różne populacje tych widłonogów stosują różne strategie adaptacyjne, np. odmienną długość cyklu życiowego, inny wiek osiągnięcia dojrzałości płciowej, czy wreszcie wielkość ciała. Ponieważ tempo rozwoju roślinożernych *Calanus* spp. jest silnie zależne od temperatury wody morskiej, dostępności pożywienia i warunków lodowych, widłonogi te są szczególnie wrażliwe na zmiany klimatyczne. Zbyt wczesne zanikanie lodu morskiego skraca okres zakwitnięcia alg, zapewniając ubogie warunki dla ich rozwoju.

Zaburzenia cykli życiowych *Calanus* spp. mogą istotnie ograniczyć ich liczebność i przesunąć w czasie szczyt ich występowania, a zatem dostępność dla drapieżników. Szczególnie narażone na te zmiany są najliczniej występujące na półkuli północnej alczyki *Alle alle*, charakteryzujące się wysoką selektywnością w wyszukiwaniu pokarmu. Te niewielkich rozmiarów ptaki morskie preferują głównie piąte stadium kopepoditowe *Calanus* spp. ze względu na jego najwyższą wartość energetyczną, która jest w stanie zrekompensować niezwykle wysokie koszty ponoszone podczas częstych i dalekich lotów żerowiskowych. Odżywiając się w morzu i rozmnażając na lądzie alczyki transportują ogromne ilości materii organicznej, nawożąc ubogą arktyczną tundrę. Wydajność karmienia młodych i sukces rozrodczy alczyków w dużej mierze zależy więc od jakości, obfitości i przede wszystkim dostępności preferowanego przez nie składnika diety.

Pomimo, że do tej pory wykazano wysoką plastyczność ptaków w stosunku do dostępności ich ofiar, przewiduje się, że wraz z dalszym wzrostem temperatury mogą one być szczególnie narażone na utratę wielu cennych żerowisk w rejonie Spitsbergenu. Praca

ta jest odpowiedzią na potrzebę dokładnego zbadania dostępności preferowanego pokarmu, czyli starszych stadiów rodzaju *Calanus*, w okresie największego zapotrzebowania energetycznego alczyka, podczas karmienia piskląt. Badania zostały zaprojektowane w oparciu o koncept dopasowania/niedopasowania (ang. match/mismatch), dotyczący zbieżności bądź rozbieżności w czasie pomiędzy cyklem życiowym drapieżnika i jego ofiary.

Pomimo, że *Calanus* spp. jest taksonem stosunkowo dobrze opisanym, wciąż niewiele jest badań dotyczących jego fenologii. W odpowiedzi na te istotne luki w wiedzy, w niniejszej pracy podjęto się dużego wyzwania logistycznego, związanego z wciąż bardzo rzadkim w Arktyce próbkowaniem opartym na odpowiednio dostosowanej, wysokiej rozdzielczości czasowej i przestrzennej. W celu poznania pełnej struktury kopepoditowej *Calanus* spp. w niniejszej pracy użyto sieci o mniejszej średnicy oczek (180µm) niż była używana dotychczas w typowych badaniach (500µm). Dane zebrane zostały trzykrotnie w ciągu dwóch kolejnych sezonów letnich (2015 i 2016), w dwóch odmiennych pod względem hydrograficznym rejonach: „atlantyckim” Kongsfjordzie i „arktycznym” Hornsundzie, w celu porównania zmienności populacyjnej na poziomie struktury kopepoditowej *Calanus* spp. w dwóch reprezentatywnych dla zachodniego Spitsbergenu obszarach. Próbkę zooplanktonu z wody zebrane zostały z powierzchniowej warstwy 50 m ze względu na zakres głębokości na jaką nurkuje alczyk (do 50 m). W ciągu dwóch lat badań, w ramach dwunastu okresów badawczych, zebrano łącznie 96 próbek zooplanktonu.

Równoległe do poboru próbek zooplanktonu prowadzono pomiary parametrów środowiskowych: temperatury, zasolenia i fluorescencji chlorofilu przy użyciu zaawansowanych technik z wykorzystaniem Laserowego Optycznego Licznika Planktonu (LOPC), sondy CTD (ang. Conductivity-Temperature-Depth sensor) oraz fluorymetru, w celu określenia, jak warunki środowiskowe wpływają na rozmieszczenie, rozmiar i dostępność *Calanus* spp. w obydwu rejonach. Wykorzystane w badaniach przyrządy dostarczyły danych o wysokiej rozdzielczości czasoprzestrzennej, stanowiąc uzupełnienie dla punktowych pomiarów prowadzonych na poszczególnych stacjach badawczych. Platforma LOPC holowana była pomiędzy stacjami badawczymi w trybie oscylacyjnym, od powierzchni do głębokości 50 m, na przełomie lipca i sierpnia, jeden raz w każdym roku w obydwu badanych rejonach.

Ponadto, w celu porównania struktury kopepoditowej *Calanus* spp. na żerowiskach i w diecie, równoległe do próbek zooplanktonu sieciowego zebrane zostały przez ornitologów z Wydziału Biologii Uniwersytetu Gdańskiego oraz Norweskiego Instytut



Polarnego (NPI) próbki diety alczyka (łącznie 132 próbki z pierwszych trzech tygodni życia piskląt) z dwóch kolonii zlokalizowanych w pobliżu morskich rejonów badawczych.

Badania przeprowadzone w ramach pracy obejmowały standardową jakościowo-ilościową analizę laboratoryjną próbek zooplanktonu z żerowisk oraz diety alczyka ze szczególnym uwzględnieniem stadiów kopepoditowych *Calanus* spp. Dodatkowo, w celu zbadania rozkładu wielkości osobników w obu badanych rejonach w relacji do temperatury, stworzono obszerną bazę pomiarów długości prosomy wszystkich stadiów kopepoditowych *Calanus* spp. z próbek zooplanktonu sieciowego obejmującą łącznie 11 388 zmierzonych osobników.

W pracy potwierdzono także, że rozkłady wielkości obu gatunków *Calanus* spp. oznaczonych na podstawie długości prosomy znacząco odbiegają od rozkładu normalnego, co wskazuje na konieczność użycia metod molekularnych do ich prawidłowej identyfikacji. Potwierdziło to także konieczność połączenia obu gatunków w jedną grupę *Calanus* spp.

Na podstawie wykonanych pomiarów wykazano, że średnia długość prosomy wszystkich stadiów kopepoditowych, z wyjątkiem dorosłych samic, jest istotnie większa w rejonie Hornsundu niż w Kongsfjordzie. Dodatkowo wykazano negatywną korelację temperatury wody morskiej z długością prosomy *Calanus* spp. oraz ze średnią wielkością organizmów zooplanktonowych. Kolejnym istotnym wynikiem była zaobserwowana w obu fiordach odmienna struktura taksonomiczna zooplanktonu. O ile w fiordzie Hornsund zaobserwowano istotną przewagę ilościową *Calanus* spp. nad innymi organizmami, to w Kongsfjordzie dominowały znacznie mniejsze taksony, takie jak *Oithona similis*, czy należące do meroplanktonu stadia larwalne *Bivalvia veliger* i *Limacina helicina veliger*. W kontekście postępującego ocieplenia klimatu, potwierdzona w niniejszej pracy przewaga mniejszych organizmów w wodach o wyższej temperaturze i w cieplejszym rejonie – Kongsfjorden, zarówno na poziomie gatunkowym jak i całego zgrupowania, jest zgodna z prognozowanym kierunkiem reorganizacji skupisk zooplanktonu.

Przy użyciu przyrządów optycznych, potwierdzono także istotny wpływ temperatury i zasolenia na rozmieszczenie *Calanus* spp. Największe skupiska z wysokim udziałem procentowym organizmów należących do tej frakcji w obydwu rejonach gromadziły się głównie w mniej zasolonej, zimnej powierzchniowej warstwie wody. Udział procentowy frakcji *Calanus* spp. był stosunkowo wysoki w obydwu latach w Hornsundzie oraz w roku 2015 w Kongsfjordzie, natomiast w roku 2016 w ostatnim rejonie zaobserwowano znacznie niższą dostępność preferowanego przez alczyki pokarmu.

W niniejszej pracy wykazano odmienną strukturę kopepoditową *Calanus* spp. zarówno przestrzenną pomiędzy dwoma rejonami, jak i między-letnią. O ile zmiany struktury kopepoditowej w Hornsundzie w obu latach przebiegały stopniowo, od przewagi wczesnych stadiów na początku lipca do dominacji piątego stadium w połowie sierpnia, o tyle w Kongsfjordzie w roku 2016 populacja *Calanus* spp. była zdominowana przez młode stadia w ciągu wszystkich trzech okresów badawczych. Obserwacje te potwierdziły, że rozwój *Calanus* spp. jest procesem niezwykle dynamicznym i wrażliwym na warunki środowiskowe, zwłaszcza w cieplejszym rejonie Kongsfjordu, będącego pod silniejszym wpływem wód atlantyckich niż Hornsund, co wskazuje na konieczność stałego monitoringu tych zmian.

Analiza składu diety alczyka potwierdziła dużą plastyczność ptaków w zdobywaniu pokarmu w obydwu rejonach, ponieważ wykazano zarówno wysoką selektywność alczyków w wyborze późnych stadiów kopepoditowych *Calanus* spp., jak i umiejętność całkowitego przestawienia się na inny, porównywalnie atrakcyjny pod względem energetycznym składnik pokarmowy. Ze względu na bliską odległość lodu morskiego w rejonie Hornsundu w sierpniu 2015 roku, główny składnik diety ptaków w tym okresie stanowił związany z lodem obunóg *Apherusa glacialis*, który zwykle stanowi jedynie uzupełniający składnik pokarmu, notowany głównie w diecie ptaków gniazdujących w rejonach północnych Spitsbergenu, zlokalizowanych bliżej marginalnej strefy lodu. Ponieważ *A. glacialis* w próbkach z sieci planktonowych występuje jedynie sporadycznie, obserwacje te potwierdziły, że skład diety alczyka w wysokim stopniu odzwierciedla warunki panujące w środowisku, w tym przypadku bliską obecność lodu morskiego i może stanowić istotne narzędzie przydatne w ocenie procesów zachodzących w środowisku morskim. Natomiast porównanie struktury kopepoditowej *Calanus* spp. na żerowiskach (w zooplanktonie) i w koloniach (diecie) alczyka wskazuje na lepszą zgodność stopnia rozwoju populacji widłonogów w rejonie Hornsundu niż Kongsfjordu, co oznacza lepsze dopasowanie w czasie, a zatem korzystniejsze warunki żerowania w chłodniejszym rejonie Hornsundu.

Istotną wartością tej pracy jest zastosowanie modelu, który prognozuje, że wzrost temperatury zgodny z obserwowanym aktualnie globalnym trendem, może doprowadzić do znacznej redukcji dostępności preferowanych przez alczyki późnych stadiów kopepoditowych *Calanus* spp., w okresie wysokiego zapotrzebowania energetycznego ich drapieżników. Wyniki modelu wskazują, że rozwój arktycznego gatunku (*C. glacialis*), będzie na tyle przyspieszony, że może doprowadzić do znacznego przesunięcia w czasie

dostępności jego piątego stadium kopepoditowego na żerowiskach. Niestety prognozy sugerują, że deficyt wysokokalorycznych, starszych stadiów, najprawdopodobniej nie będzie rekompensowany przez stowarzyszony z wodami atlantyckimi, ciepłolubny gatunek bliźniaczy (*C. finmarchicus*), ponieważ rozmnażając się wielokrotnie w ciągu sezonu, będzie on utrzymywał głównie młodą populację w powierzchniowej warstwie wody. Poczynione w niniejszej pracy obserwacje *in situ* wraz z modelowymi obliczeniami wskazują, że struktura kopepoditowa *Calanus* spp. zmienia się znacznie bardziej dynamicznie w Kongsfjordzie, który jest pod silniejszym wpływem adwekcji ciepłych wód atlantyckich niż w chłodniejszym Hornsundzie. Wyniki te wpisują się w prognozowany trend skracania długości trwania cykli *Calanus* spp. przy jednoczesnym wydłużaniu sezonu wysokiej produkcji pierwotnej.

Przeprowadzone w ramach rozprawy doktorskiej obserwacje potwierdziły konieczność kontynuowania sezonowych badań fenologii *Calanus* spp. w wodach Svalbardu, a także stałego monitorowania odpowiedzi alczyka na te zmiany. Przeprowadzone w niniejszej pracy prognozowanie dotyczące ograniczenia liczebności, rozmieszczenia, a w konsekwencji i dostępności dla planktonożerców - *C. glacialis* na rzecz *C. finmarchicus*, wskazało na potrzebę wykorzystania metod molekularnych w przyszłych badaniach, w celu określenia dokładnego udziału obu gatunków na żerowiskach oraz w diecie alczyków, zarówno w przyszłości, jak i na bazie dostępnych materiałów historycznych. Prawidłowa identyfikacja tych dwóch głównych składników diety pozwoli lepiej zrozumieć zakres plastyczności alczyków względem dostępności ich ofiar na przestrzeni ostatnich dekad, w dynamicznie zmieniającym się środowisku arktycznym.

## SUMMARY

One of the fastest and the most spectacular effects of the global warming are observed currently in the Arctic. The increase in sea surface temperature and intensified inflow of waters of Atlantic origin disrupt the water masses formation and frontal zones processes, contributing to both local and large-scale environmental changes. The size, composition and timing of biological production and turnover are significantly affected by the diminishing/lack of ice, higher seawater temperatures or disruptions in stratification.

The scenarios of pelagic food web modifications due to the increased seawater temperature indicate that the importance of smaller boreal species will increase significantly in the higher latitudes and may even exceed the importance of larger, typical Arctic organisms. Significant environmental changes, such as e.g. elevated temperatures, most probably will cause the intra-species body size reduction. Until recently it has been predicted that species and size shifts would have negative consequences for top predators, however new studies suggests that energy transfer to higher trophic levels may be more efficient than previously assumed. Unfortunately, such an optimistic scenario may not apply to strictly specialized visual predators, such as planktivorous seabirds.

In the context of dynamic changes shaping Arctic marine environment, it is important to monitor their impact on marine organisms, in particular *Calanus* copepods, which due to their high energy content are key species in the Arctic pelagic ecosystems. Three main herbivore *Calanus* species dominate the mesozooplankton biomass in the Arctic Ocean: *C. glacialis*, *C. finmarchicus* and *C. hyperboreus*. *Calanus glacialis* and *C. finmarchicus* are the target species of this dissertation because of their predominance in Svalbard waters and in little auks' diet.

The high importance *Calanus* spp. in marine ecosystem functioning is based on their role in a transfer of omega-3 fatty acids, which are crucial for growth and reproduction of all marine organisms. Even 60% of their body volume is filled with lipids that are stored in special sacs. Until recently, the amount of lipids was suggested to be species-dependent and the higher lipid storage was attributed to larger, Arctic *C. glacialis* compared to smaller, less energetically profitable boreal *C. finmarchicus*. This approach emphasized different role of both species in the Arctic ecosystem. However it is already known that the lipid content is actually dependent mainly on body size. Most probably, this misunderstanding results of the misidentification of both, morphologically very similar species, which so far

have been distinguished mainly on the basis of the prosome length. Molecular tools used in recent studies showed however that size ranges of *C. glacialis* and *C. finmarchicus* overlap and are generally much broader than previously assumed. Therefore, due to the proven similar function of both species and difficulties in distinguishing them properly, for the purposes of this thesis *C. glacialis* and *C. finmarchicus* have been classified into one - *Calanus* spp. group.

Depending on environmental conditions, different populations of *Calanus* spp. apply various life strategies, e.g. different length of the life cycle, age of maturation, or body size. Since the development rate of *Calanus* spp. highly depends on the seawater temperature, ice conditions and food availability these copepods are especially sensitive to climate changes.

Disruption in life cycles of *Calanus* spp. may significantly reduce their abundance and shift their peak of occurrence, and therefore availability for predators. Little auks, the most numerous seabirds in the northern hemisphere, are very sensitive for such changes. They actively select larger, older life stages of *Calanus* spp. individuals. Feeding in the sea and breeding on land they transport a huge amount of organic matter fertilizing poor Arctic tundra. The temperature increase, providing favorable conditions for laying eggs, shift the period of little auks' high energy demands. The efficiency of their reproductive success and feeding chicks largely depends on the quality, abundance and, above all, the availability of their main diet component.

Despite the flexible foraging behavior of little auks it is predicted that the negative impact of warming in a form of the loss of suitable feeding grounds in Spitsbergen is sooner or later inevitable. This work is a response to the need to investigate thoroughly the relationship between the availability of the preferred food, i.e. the older life stages of *Calanus* spp., and the period of the little auks highest energy demands during chicks rearing period. The research hypothesis was based on the match/mismatch theory regarding the relationship between the timing of predator and its prey.

Although *Calanus* spp. is a relatively well known taxon, still very few studies have been focused on their phenology. This dissertation addresses these major gaps in knowledge by taking an effort of the logistical challenging high temporal and spatial resolution sampling, which is still very rare in the Arctic. In addition, in order to study the full copepodite structure of *Calanus* spp. a net with a smaller mesh size (180 $\mu$ m), instead of standard (500 $\mu$ m) was used. In order to compare the population variability over time at the level of copepodite structure *Calanus* spp. in the two representative for western

Spitsbergen regions data were collected three times over two successive summer seasons (2015 and 2016), in two hydrographically different regions: “Atlantic” Kongsfjorden and “Arctic” Hornsund. Seawater zooplankton samples were collected from the surface 50 m water layer as is the maximum depth range of little auks diving. Over two years of research, 96 seawater zooplankton samples were collected and analysed.

To determine the relation between environmental conditions and the distribution, size and availability of *Calanus* spp. in both regions, simultaneously to zooplankton sampling, environmental parameters: temperature, salinity and chlorophyll fluorescence were measured using high-resolution instruments: Laser Optical Plankton Counter (LOPC), Conductivity-Temperature-Depth sensor (CTD) and fluorometer. The LOPC-CTD-F platform was towed between the zooplankton stations in oscillating mode from the surface to the depth of 50 m at the turn of July and August, once in each year in both studied regions.

In addition, to compare the copepodite structure of *Calanus* spp. on the foraging grounds and in the diet, simultaneously to the seawater zooplankton samples, the little auks’ diet samples (132 samples from the first three weeks of chicks’ life) were collected by ornithologists from the University of Gdansk and the Norwegian Polar Institute (NPI) from two colonies located near both marine research areas.

The study included a standard quality-quantitative laboratory analysis of zooplankton samples from foraging grounds and the little auks’ diet with particular emphasis on the copepodite stages of *Calanus* spp. In addition, to investigate the size ranges of individuals in both study regions in relation to seawater temperature, an extensive database of prosome length measurements for all copepodite stages of *Calanus* spp. including 11 388 measured individuals was created from the seawater zooplankton samples.

The results have demonstrated that neither the size of specimens classified as *C. glacialis* nor *C. finmarchicus*, determined on the basis of their prosome length, were following a normal size distribution, which indicated the need to use molecular methods for their correct identification. This confirmed the difficulty in proper species recognition and was important argument for the putting the two species in one *Calanus* spp. category.

On the basis on conducted morphometric analyses, it was found that the mean prosome length of all copepodite stages, with the exception of adult females, was significantly higher in Hornsund than in Kongsfjorden. In addition, the seawater temperature were proved to be negatively correlated with the *Calanus* spp. prosome lengths



and the mean size of zooplankton organisms. Another significant result was the different taxonomic structure of zooplankton observed in both fjords manifested in substantial domination of *Calanus* spp. in Hornsund and higher share of small taxa like *Oithona similis*, *Bivalvia* veliger and *Limacina helicina* veliger in Kongsfjorden. In the context of progressive global changes, the dominance of smaller organisms in the warmer region – of Kongsfjorden observed in this work, is consistent with the predicted direction of reorganization of zooplankton communities.

The temperature and salinity were found to have significant effect on the distribution of *Calanus* spp. The main patches with a high percentage of *Calanus* spp. fraction in both regions were mainly concentrated in less saline, cold water layer. The percentage of *Calanus* spp. fraction was relatively high in both years in the Hornsund and only in 2015 in Kongsfjorden, because in 2016 much lower contribution of this preferred by little auks prey was observed in this region.

Dissertation results show different copepodite structure of *Calanus* spp. between both two regions and between the two years. While the development of the copepodite structure in Hornsund in two studied years progressed gradually, from the predominance of early stages at the beginning of July to the dominance of the fifth stage in mid-August, in the Kongsfjorden in 2016 the population of *Calanus* spp. was dominated by early stages during all three research periods. These observations confirmed that the development of *Calanus* spp. is an extremely dynamic and sensitive for environmental conditions processes, especially in the warmer Kongsfjorden, which is more influenced by Atlantic waters than Hornsund. These results indicate the need for constant monitoring of such changes.

The analysis of the little auks' diet composition points towards their high foraging plasticity in both regions, since even though they were consequently selecting late copepodite stages of *Calanus* spp., they were also able to switch to quite different, but comparatively attractive in terms of energy content prey. Due to the close distance of sea ice in the Hornsund area in August 2015, the main component of the seabirds diet during this period was the ice-associated *Apherusa glacialis*, which is usually only a supplementary component of the little auks' diet found mainly in the diet of seabirds nesting in more northern regions, located closer to marginal ice zone. Since *A. glacialis* is very rarely found in planktonic nets, these observations proved that sometimes the composition of the little auks' diet can be a better predictor for studying the actual state of the marine environment. On the other hand, the comparison of the copepodite structure of *Calanus*

spp. on feeding grounds and in little auks' diet indicates a better match between the development level of the copepods in the Hornsund region than in Kongsfjorden, and therefore more favorable feeding conditions in the colder Hornsund region.

The important value of this work is the use of a model that simulates the *Calanus* spp. development in the warming scenario. The model predicts that the seawater temperature increase, consistent with the currently observed global trend, will lead to a significant reduction in the availability of the late copepodite stages of *Calanus* spp. preferred by the auks, during the period of their highest energy demands. The results of the model indicate that the accelerated development of the Arctic species (*C. glacialis*), can cause a significant shift in time of availability of its fifth copepodite stage in the foraging grounds. Unfortunately, the prognosis suggests that the deficit of high-caloric older stages is unlikely to be compensated by the sibling Atlantic species (*C. finmarchicus*), since it will maintain mainly the young population in the surface layer of water. The observations made in this work together with the model calculations indicated that the copepodite structure of *Calanus* spp. will change much more dynamically in Kongsfjorden, which is more strongly influenced by the advection of warm Atlantic waters than in the colder Hornsund. These results are in line with the projected trend of shortening the life span of *Calanus* spp. along with the climate change.

The results of this dissertation confirmed the hypothesis of the possible mismatch in timing between the availability of *Calanus* spp. CV and the little auks highest food demands. Therefore the findings and raised predictions highlight the necessity to continue further seasonal studies of *Calanus* spp. phenology in Svalbard waters, as well as to monitor constantly the response of the little auk to these ongoing changes. The predicted decrease in availability of *Calanus* spp. for planktivores, indicated the need to determine the real ratio of both species on the foraging grounds and in little auks' diet, which nowadays can be assessed only using molecular methods. The proper identification of these two main components of the little auks' diet will allow to better understand their ecological plasticity in the dynamically changing Arctic environment and thus how their response would be propagated along the food chain.



# 1. INTRODUCTION

## 1.1 ZOOPLANKTON IN THE WARMING ARCTIC

The fastest and the most spectacular effects of the global warming are observed in the Arctic in recent years (IPCC 2014; Shepherd 2016; Piskozub 2017). The increase in sea surface temperature and intensified inflow of waters of Atlantic origin disrupts the processes frontal zones and water masses formation, contributing to changes in climatic conditions and hydrography (Blindheim et al. 2000; Schauer et al. 2004; Walczowski et al. 2012, 2017). Changing environmental conditions impact the life of many marine organisms (Brierley and Kongsfjord 2009; Post 2017; Beaugrand and Kirby 2018). The size, composition and timing of biological production and turnover must respond to the lack of ice, higher seawater temperatures or modifications in stratification (Hoegh-Guldberg and Bruno 2010; Moore et al. 2018).

Climate warming leads to alteration of the zooplankton community size structure, which is considered to be more important than shifts in biomass (Richardson and Schoeman 2004; Lane et al. 2008). The scenarios of pelagic food web modifications due to the increased seawater temperature indicate that smaller boreal species will have increasingly important roles in the higher latitudes (Beaugrand et al. 2002; Wassmann et al. 2011; Renaud et al. 2018). Northward expansion of organisms better adapted to warm water conditions is already observed (Woodworth-Jefcoats et al. 2016; Gluchowska et al. 2017a; Haug et al. 2017). Changing environmental conditions affect also intra-species size variability (Parent et al. 2011; Gabrielsen et al. 2012; Choquet et al. 2018; Renaud et al. 2018), eg. the increasing temperature significantly affects the *Calanus* spp. body size reduction (Campbell et al. 2001) and it is predicted that, this process will systematically proceed with further climate warming (Banas et al. 2016; Renaud et al. 2018). Until recently it has been predicted that body-size shifts will have negative consequences for top predators, however it is already know that energy transfer to higher trophic levels may be more efficient than previously assumed (Renaud et al. 2018). Unfortunately, such an optimistic scenario may not apply to strictly specialized visual predators, actively selecting mainly larger *Calanus* spp. individuals, such as the little auk (Kidawa et al. 2015).

## 1.2 CALANUS SPP. IN THE ARCTIC FOOD WEB

Three main herbivore *Calanus* species: *Calanus glacialis*, *C. finmarchicus* and *C. hyperboreus* dominate the mesozooplankton biomass in the Arctic Ocean (Mumm et al. 1998; Hop et al. 2006; Wassmann et al. 2006; Błachowiak-Samołyk et al. 2008; Søreide et al. 2008; Carstensen et al. 2012; Aarflot 2017). Their characteristics cover different life-history strategies and centers of distribution, thus they are influenced by different environmental forcing (Scott et al. 2000; Falk-Petersen et al. 2002, 2009; Daase et al. 2007, 2013; Melle et al. 2014). *Calanus glacialis* is a typical Arctic shelf-associated species (Jaschnov 1970; Conover 1988; Kosobokova 1998), generally larger than its counterpart, *C. finmarchicus* distributed mainly in the North Atlantic (Jaschnov 1970; Hirche 1991; Planque et al. 1997; Hirche and Kosobokova 2007). *Calanus glacialis* and *C. finmarchicus* are the target species of this dissertation because of their predominance in Svalbard waters (eg. Gluchowska et al. 2016). The largest *C. hyperboreus* is mainly deep-water, oceanic species (Conover 1988; Hirche 1991; Kosobokova & Hirche 2009), very rarely caught in planktonic nets dedicated for sampling mesozooplankton fraction (Błachowiak-Samołyk et al. 2017). *Calanus* spp. are a key link between primary producers and higher trophic levels in Arctic and sub-Arctic marine food webs (Varpe et al. 2005; Steen et al. 2007; Karnovsky et al. 2008; Lee et al. 2006; Falk-Petersen et al. 2002, 2007, 2009; Renaud et al. 2012) and constitute important food source for macrozooplankton (Scott et al. 1999; Falk-Petersen et al. 2002; Hop et al. 2006; Kraft et al. 2013), fish (Helle and Pennington 1999; Dalpadado et al. 2000; Varpe et al. 2005; Hop and Gjørseter 2013; Nahrgang et al. 2014), marine mammals (Pomerleau et al. 2012) and seabirds (Weslawski et al. 1999; Dahl et al. 2003; Karnovsky et al. 2003; Steen et al. 2007).

The important role of *Calanus* spp. in marine ecosystem functioning is based on the transfer of omega-3 fatty acids (long-chain PUFAs produced by marine algae), which are crucial for growth and reproduction of all marine organisms (Ackman 1989). High-energy wax ester lipids are converted by these copepods from proteins and low-energy carbohydrates deriving directly from algae (Lee et al. 2006; Falk-Petersen et al. 2009). They contain up to 50% – 70% of lipids in dry mass (Falk-Petersen et al. 1990, 2009). Even 60% of their body volume is filled with lipids stored in lipid sacs (Sargent and Falk-Petersen 1988; Miller et al. 2000; Lee et al. 2006). Until recently, the amount of lipid was suggested to be species-dependent and the higher lipid storage was attributed to larger Arctic *C.*

*glacialis* compared to smaller, less energetically profitable boreal *C. finmarchicus* (Scott et al. 2000; Falk-Petersen et al. 2009). This approach emphasized different role of both species in the Arctic ecosystem (Falk-Petersen et al. 2007; Kwasniewski et al. 2010; Reygondeau and Beaugrand 2011; Wassmann et al. 2011). However it is already known that the lipid content is actually dependent largely on body size (Renaud et al. 2018). Most probably, this misunderstanding results of the misidentification of both, morphologically very similar species, which so far have been distinguished mainly on the basis of the prosome length (Kwasniewski et al. 2003). However molecular tools used in recent studies showed that size ranges of *C. glacialis* and *C. finmarchicus* overlap and are generally much broader than previously assumed (Parent et al. 2011; Gabrielsen et al. 2012; Nielsen et al. 2014; Choquet et al. 2018; Renaud et al. 2018). Therefore, due to the proven similar function of both species and difficulties in distinguishing them properly, for the purposes of this thesis *C. glacialis* and *C. finmarchicus* have been classified into one - *Calanus* spp. group.

### **1.3 CALANUS SPP. LIFE CYCLE**

Depending on environmental conditions, different populations of *Calanus* spp. apply various life strategies, e.g. different length of the life cycle, body size or age of maturation (Falk-Petersen et al. 2009). *Calanus* spp. is able to extend the breeding season beyond short periods of high primary production to optimize its growth and development (Varpe et al. 2007; Varpe 2012).

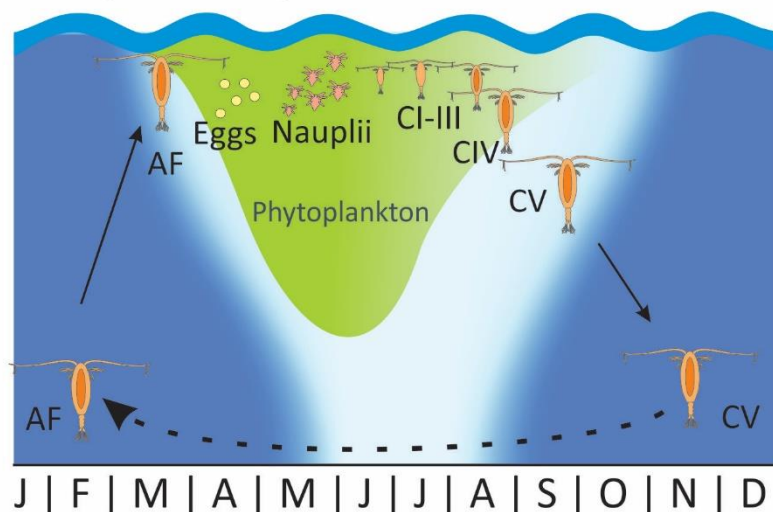
*Calanus glacialis* develops in seasonal ice covered waters (Jaschnov 1970; Daase et al. 2007; Błachowiak-Samołyk et al. 2008; Søreide et al. 2008) with highly variable food supply (Kubiszyn et al. 2014), where it adjust the length of its cycle to 1-2 years (Fig.1) depending on the prevailing environmental conditions (Tande 1985; Melle and Skjoldal 1998; Arnkværn et al. 2005; Falk-Petersen et al. 2007, 2009). Its breeding period is closely linked to the two main peaks of primary production: earlier - ice algal bloom and later - phytoplankton bloom (Fig. 1; Søreide et al. 2010; Ji et al. 2013). During spring and summer *C. glacialis* is feeding intensively and molting (at different rates, depending on seawater temperature and food availability) by successive life stages, consisting of six nauplii and six copepodite stages. In autumn, older copepodites (CIV and CV) are preparing to overwintering and descent to deeper water layers. The huge amounts of fat collected during summer help them to survive in hibernation in the depths the severe season until they ascend to the surface in spring to reproduce again (Kosobokova 1999). Due to lipid-based

reproduction it can start to spawn prior to phytoplankton bloom since it can use its lipid reserves to fuel maturation and egg production (capital-breeder strategy; Varpe et al. 2009, Søreide et al. 2010). Since the life cycle of *C. glacialis* mainly depends on the sea ice conditions in a given year, changes in the range and time of ice formation can lead to mismatch between ice algal/phytoplankton blooms and copepod reproductive period (Søreide et al. 2010; Banas et al. 2016). Too early ice breakup shortens the period of ice algal blooms, providing poor conditions for zooplankton development (Leu et al. 2011; Daase et al. 2013; Post et al. 2017).

Boreal *Calanus finmarchicus* has 1-year life cycle (Fig. 1) in the Arctic (Madsen et al. 2001; Arnkværn et al. 2005; Scott et al. 2000) however it can produce several generations per year in southern areas of its northern distribution range (Durbin et al. 2000; Miller et al. 2000). In contrast to *C. glacialis* its maturation and development are dependent on continuous food supply since it represents food-dependent reproduction (income-breeder strategy; Ji et al. 2012). Thus reproduction events of *C. finmarchicus* usually tend to occur during the second peak of primary production, phytoplankton bloom (Fig. 1; Hirche et al. 1997; Niehoff et al. 2002; Madsen et al. 2008; Swalethorp et al. 2011; Kjellerup et al. 2012). Studies conducted so far indicate a better physiological adaptation to climate change in boreal species such as *C. finmarchicus*, which, because of the rapid response to dynamic processes of phytoplankton blooms, can win the competition with more Arctic organisms and replace them (Weydmann et al. 2015; Renaud et al. 2018).

Dynamic changes in the environmental conditions and timing of primary production (Kubiszyn et al. 2014) cause high variability in the development rate and length of life cycles of *Calanus* spp. In this context, there are still insufficient studies on their phenology, which are based mostly on episodic measurement during the summer season. Such investigations require a high frequency of sampling, which is still logistical challenge in harsh Arctic conditions.

### One-year life cycle



### 1-2 year life cycle

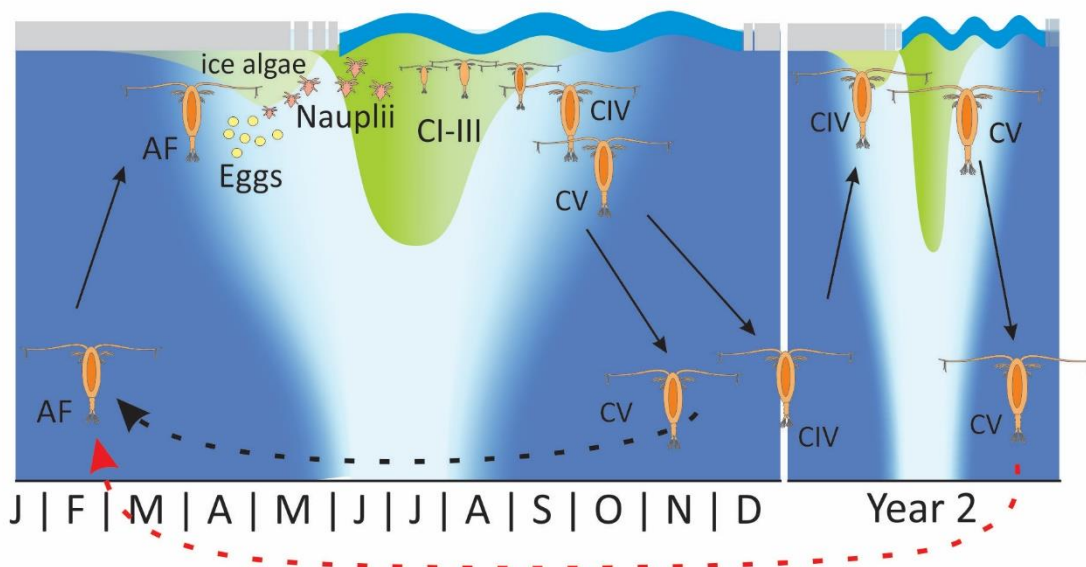


Fig. 1. Scheme of *Calanus* spp. life cycles. One-year life cycle as commonly displayed by *C. finmarchicus* in ice-free waters; and 1-2 year life cycle as commonly displayed by *C. glacialis*. Copepodite stages – CI-CV; adult females – AF. Solid black arrows: ontogenetic seasonal migration; hatched red and black arrows connect the cycle. Below the bottom axis: abbreviations of the subsequent names of the months comprising one full year starting from January (J). Illustration: Maline Daase.

## 1.4 PREY-PREDATOR INTERACTION UNDER CHANGING CLIMATE

Changes in abiotic factors constrain also timing of marine organisms leading to phenological cascades in food webs (Post 2017). The rate and level of response of organisms belonging to different functional groups and trophic levels is usually different and can significantly alter the trophic interactions (Edwards and Richardson 2004; Chivers 2017). Particularly vulnerable to these changes are higher trophic levels, highly dependent on the timing of primary and secondary producers. Fluctuations in planktonic production may lead to disturbance in interactions between predators and prey (match/mismatch; Hjort 1914; Cushing 1990) and as a consequence may severely disrupt the functioning of the whole ecosystem (Stenseth et al. 2002; Both et al. 2006; Hipfner 2008).

Very sensitive for environmental changes are high-latitude nesting seabirds, in which life cycle is strongly depended on food resources in the sea (Durant et al. 2004; Jakubas et al. 2016a, 2017). It has been shown that the quality of zooplanktivorous seabirds' diet is affected by the abundance of their prey, but also by their timing (Hipfner 2008). Little auk, the keystone planktivorous seabird in the Arctic (Stempniewicz 2001) is particularly vulnerable to these changes, due to the high selectivity of its prey (Enstipp et al. 2018). It actively capture mainly the fifth copepodite stage (CV) of *Calanus* spp. which provides the most nutritional food base for the little auk (Mehlum and Gabrielsen 1993; Weslawski et al. 1999, 2006; Planque and Batten 2000; Pedersen and Falk 2001; Karnovsky et al. 2003; Wojczulanis et al. 2006; Jakubas et al. 2007, 2011; Hovinen et al. 2014; Boehnke et al. 2015, 2017). The breeding period of the birds, linked with the highest energy demand (Konarzewski et al. 1993), occurs in a narrow range of short Arctic summer. Therefore, the response of *Calanus* spp. to climate change, their main prey, is crucial for the survival of little auk. The observations conducted so far have suggested some plasticity of the little auks in relation to the availability and/or timing of prey and changing environmental conditions (Grémillet et al. 2012; Jakubas et al. 2016b; Møller et al. 2018) however the range of this plasticity has not been fully recognized yet (Jakubas et al. 2017). To maximize their fitness during chick rearing period, little auks adopt bimodal foraging strategy adjusting the length and frequency of long and short trips to the conditions prevailing on foraging grounds (Steen et al. 2007; Welcker et al. 2009; Hovinen et al. 2014; Jakubas et al. 2012, 2014). Little auks are known to feed also on e.g. ice-associated amphipod *Apherusa glacialis* (Kwasniewski et al. 2010; Jakubas et al. 2011; Boehnke et

al. 2015, 2017) however, they had to fly to the very distant marginal ice zone for this diet item. Despite the flexible foraging behavior and the fact that no clearly negative effects of changes in the availability of food on the survival of the little auks and their reproductive success have been observed so far (Grémillet et al. 2012; Jakubas et al. 2016b, 2017; Møller et al. 2018), it is predicted that the negative impact of warming on the loss of suitable feeding grounds is sooner or later inevitable (Jakubas et al. 2017). Therefore, the study of the phenology of the main prey of little auk is very important in the context of understanding the threats and forecasting the future for this important seabird species in the Arctic. Although a high-resolution research on the phenology of *Calanus* spp. in the context of the food demand for a little auk was recently conducted on Greenland (Møller et al. 2018), this problem has not yet been sufficiently investigated on Svalbard (Jakubas et al. 2016a).



## 1.5. AIMS AND OBJECTIVES

The main objective of this thesis is to investigate the complete copepodite structure of *Calanus* spp. in the context of high and variable food demand of the little auk *Alle alle* - the key seabird species in the Arctic ecosystem under changing environmental conditions. Additional dissertation aim was to predict the phenology of *Calanus glacialis* and *C. finmarchicus* in very probable, future warming scenarios. The study design was assumed to test the match/mismatch concept regarding timing of the peak of the abundance of preferable prey (zooplankton) with the highest energy requirement of a planktivorous predator (little auk) during three summer periods corresponding to seabirds' chick rearing period.

The main objectives of the dissertation are expressed as the following research questions:

- 1) How does the copepodite structure of *Calanus* spp. differ in two hydrographically different regions and summer seasons?
- 2) How does the size of mesozooplankton differ along with seawater temperature at both the community and individual (*Calanus* spp. fifth copepodite stage) levels?
- 3) What is the spatial distribution of *Calanus* spp. in relation to different environmental factors in two hydrographically different regions and various summer seasons?
- 4) What would be the composition of two *Calanus* species (*C. glacialis* and *C. finmarchicus*) copepodite structures predicted under the scenario of seawater temperature increase?
- 5) Are the variability in *Calanus* spp. copepodite structure and availability reflected in little auks' diet?



## 2. MATERIAL AND METHODS

### 2.1. STUDY AREA

Research was conducted on the west coast of Spitsbergen in two fjords, representing different hydrographic regimes: northerly located Kongsfjorden and Hornsund in the south (Fig. 2). Hornsund area is situated on the south-western tip of Spitsbergen and is affected mainly by the coastal Sørkapp Current carrying less-saline, cold Arctic water (Cottier et al. 2005; Prominska et al. 2017). Kongsfjorden is influenced by warmer Atlantic Water of the West Spitsbergen Current (WSC; Saloranta and Svendsen 2001; Nilsen et al. 2008; Piechura and Walczowski 2009; Kwasniewski et al. 2010; Prominska et al. 2017). The two different currents are separated by density gradient and form the large frontal system along the West Spitsbergen Shelf (WSS; Saloranta and Svendsen 2001; Cottier and Venables 2007; Sakshaug et al. 2009). In the recent years the gradual warming is observed in both fjords. Two times greater transport of warm Atlantic Water is observed however in Kongsfjorden, with 1°C higher water temperature and 0.5 higher salinity compared to Hornsund. Hornsund faces two times higher freshwater content (Prominska et al. 2017). Additionally, both fjords differ significantly in terms of bathymetry with maximum of 150 m depth compared to almost 400 m, at the entrance of Hornsund and Kongsfjorden, respectively (Prominska et al. 2017).

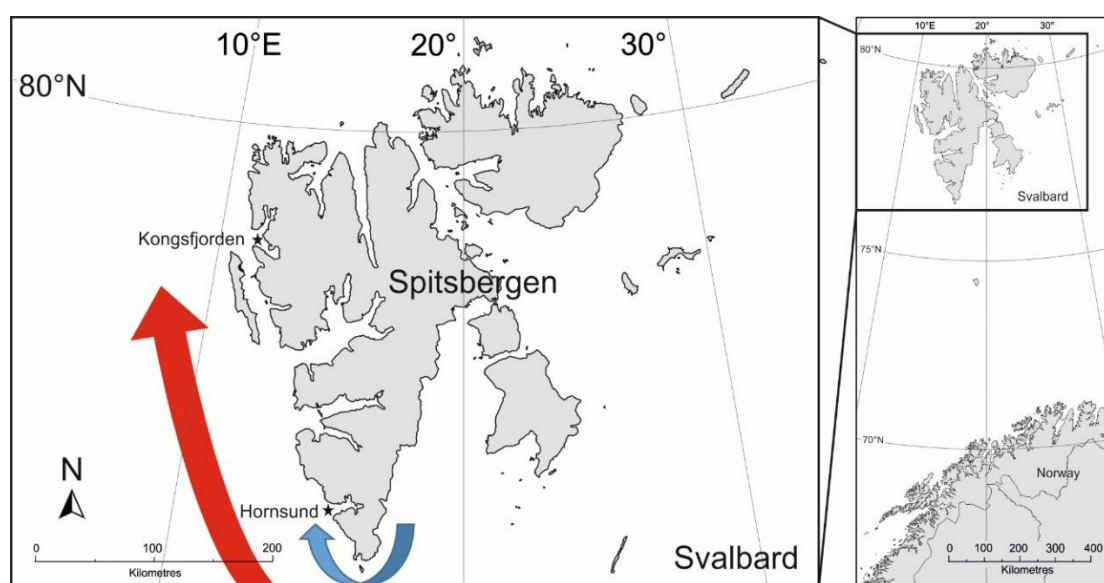


Fig. 2. Map of the study area with current patterns in the Spitsbergen region (simplified from Sakshaug et al. 2009).

## 2.2. SAMPLING PROTOCOL

### Net samples

Zooplankton samples from the little auk foraging grounds were taken during two summer seasons (hereafter study season) of 2015 and 2016 (Table 1, Fig. 3). Each year they were taken in two hydrographically different study locations of “cold” Hornsund and “warm” Kongsfjorden, each time in the inner part of the fjord in the adjacent areas located on the WSS (Fig. 3). In Hornsund samples were collected three times during each season, (hereafter study periods): 3, 13 and 7 samples in 2015 (hereafter respectively H1, H2, H3) and 5, 15, 7 in 2016 (respectively H1', H2', H3'). In Kongsfjorden 9, 5, 6 samples were collected in 2015 (hereafter respectively K1, K2, K3) and 9, 8, 9 in 2016 (K1', K1.5', K2'). For exact sampling dates see Table 1. In total, during twelve zooplankton sampling campaigns 96 zooplankton samples were collected: 50 in Hornsund area, and 46 in Kongsfjorden area. Most of the sampling was performed directly from the R/V *Oceania*. (IO PAN). Two sampling campaigns in Kongsfjord area (K1 and K2') were done on board of R/V *Lance* (Norwegian Polar Institute), one on board Zodiac boat (K3 in 2015) and one in Hornsund on board S/Y Magnus Zaremba (H3' in 2016). Most of the samples (74) were collected using WP2-type net (0.25 m<sup>2</sup> opening area) fitted with filtering gauze of 180 µm mesh size. Seventeen samples (K1 in 2015 and K1.5' in 2016) were collected using WP2-type net with 200 µm mesh size. Five samples (K2) were collected using WP2-type net with 60 µm mesh size. Zooplankton was collected from mid-surface water layer (i.e. upper 50 m) during each sampling. This water layer was arbitrary chosen taking into consideration the little auk maximal diving depth of 50 m (Amélineau et al. 2016a). After collection all samples were preserved in 4% formaldehyde solution in borax-buffered seawater and transported to laboratory for analysis

Table 1. Little auks' foraging grounds sampling dates in two fjords. Codes for sampling in Hornsund: H1, H2, H3 in 2015 and H1', H2', H3' in 2016. Codes for sampling in Kongsfjorden: K1, K2, K3 in 2015 and K1', K1.5', K2' in 2016. Within H2 "a" and "b" stands for comparison with diet samples (Hc1, Hc2) as separated study periods.

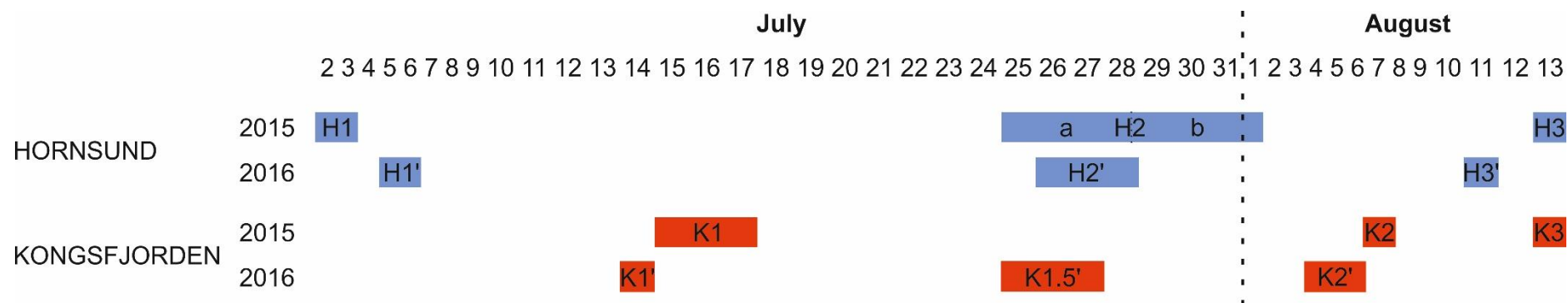
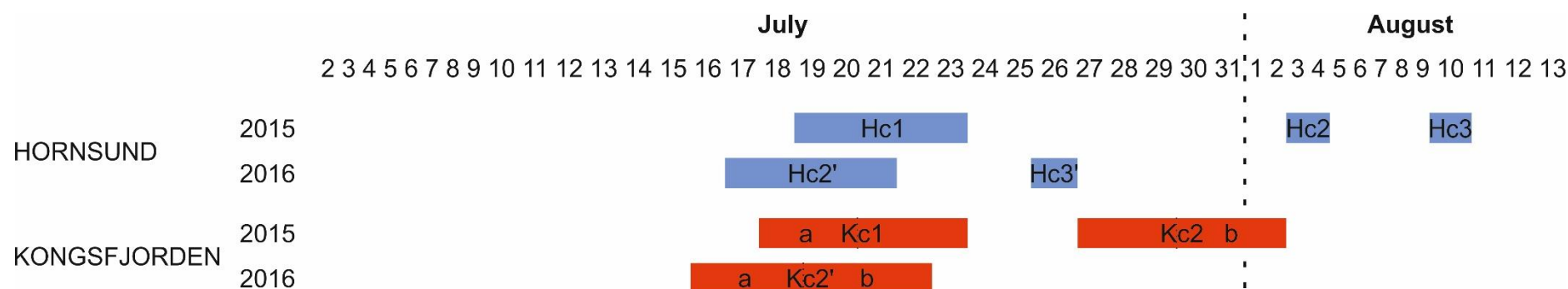


Table 2. Sampling dates from the little auks' colonies located in two fjords. Codes for sampling in Hornsund colony: Hc1, Hc2, Hc3 in 2015 and Hc2', Hc3' in 2016. Codes for sampling in Kongsfjorden Kc1, Kc2 in 2015 and Kc2' in 2016. Within Kc1, Kc2 and Kc2' "a" and "b" stands for comparison with seawater zooplankton samples (K1, K2, K1', K1.5') as separated study periods.



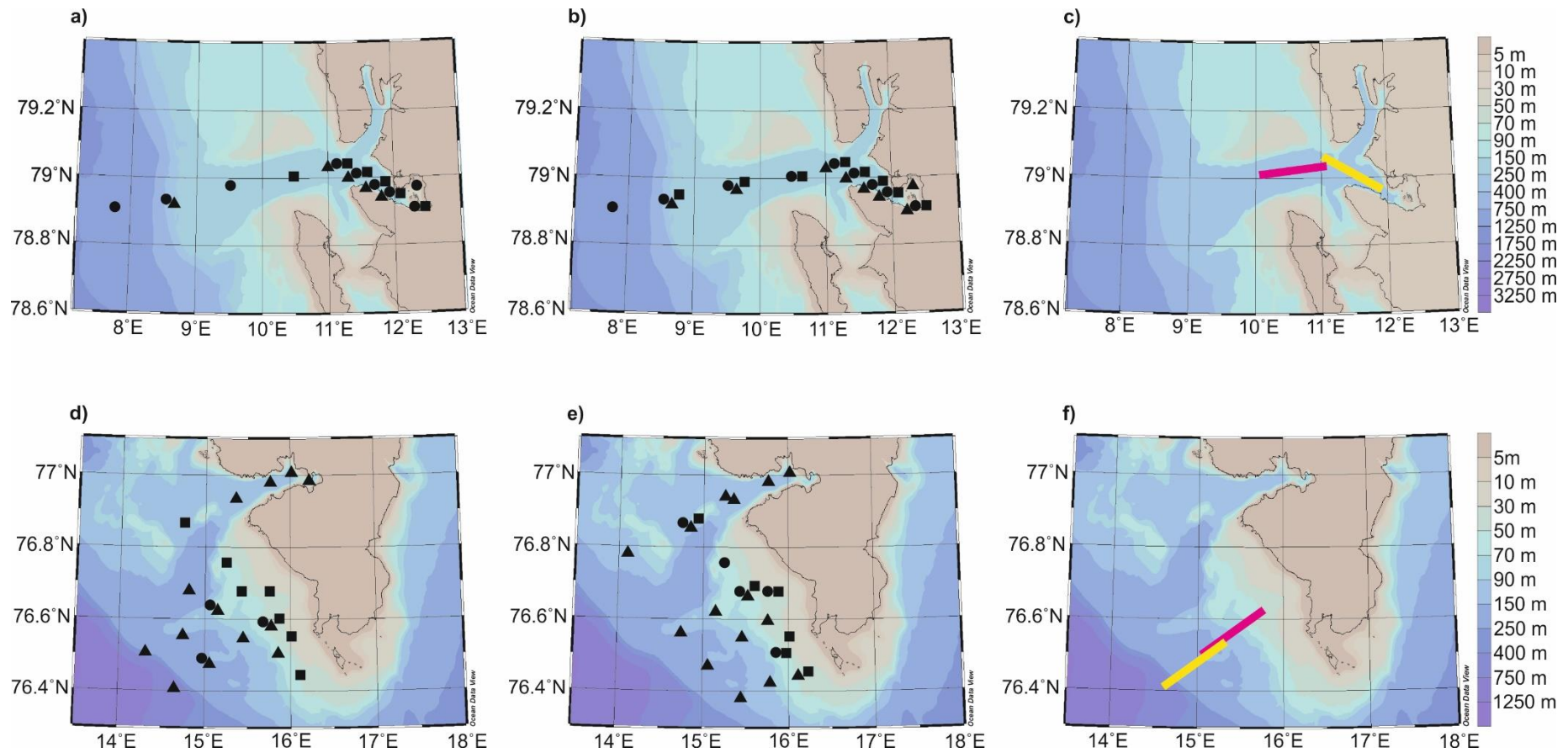


Fig. 3. Zooplankton sampling stations and bathymetry in two years in Kongsfjorden (a 2015, b 2016, c 2015 & 2016) and Hornsund area (d 2015, e 2016, f 2015 & 2016) marked with circles (first sampling study period K1, K1', H1, H1'), triangles (second sampling study period K2, K1.5', H2, H2') and squares (third sampling study period K3, K2', H3, H3'). The area of Laser Optical Plankton Counter (LOPC) surveys in Kongsfjorden (c) and Hornsund (f) are marked with lines (yellow in 2015, pink in 2016).

## **Diet samples**

Diet samples are the food loads collected from the adult little auks carrying food to their chicks. Birds were captured in each colony with mist nets or noose-carpets in two colonies: in Hornsund and in Kongsfjorden. The food content was gently scooped out of the little auk's gular pouch using a small spoon. Birds were released after 5–10 min of handling. To avoid recapture of the same individual, the birds were marked. Each food load were put into a separate plastic container and preserved in 4% formaldehyde solution in seawater. Diet samples were collected 5 times in Hornsund: 3 times in 2015 (hereafter Hc1, Hc2 and Hc3, c-colony) and 2 times in 2016 (Hc2' and Hc3'), 3 times in Kongsfjordens: 2 times in 2015 (Kc1, Kc2) and 1 time in 2016 (Kc2'). The names of the study periods were given according to the week of little auks' chicks life calculated on the basis of the median hatching date (Jakubas et al. 2013, 2016a). For exact sampling dates see Table 2. In total there were 32, 21, 10 samples in 2015 and 20, 20 in 2016 in Hornsund, while in Kongsfjorden 8, 7 samples in 2015 and 14 samples in 2016.

## **Environmental variables and distribution of *Calanus* spp. fraction**

The measurements of temperature, salinity, chlorophyll fluorescence and distribution of *Calanus* spp. fraction were conducted with the use of instrument platform equipped with a Conductivity-Temperature-Depth sensor (CTD; SBE 911plus, Seabird Electronics Inc.), fluorometer (F; Seapoint SensorsInc.) and Laser Optical Plankton Counter (LOPC Conductivity Temperature, Brooke Ocean Technology Ltd.). The LOPC-CTD-F platform was towed in an undulating mode oscillating between surface and 50-m depth. By equipping the platform with a CTD and a fluorometer, the information of the structure of plankton was delivered concurrently with environmental variables. The LOPC is an in situ sensor which provides data on abundance and size structure of plankton community by measuring each particle passing through the sampling tunnel of 49 cm<sup>2</sup> cross section. As the particle passes the sensor, the portion of blocked light is measured and recorded as a digital size and converted to equivalent spherical diameter (ESD). ESD is a diameter of a sphere that would represent the same cross-sectional area as the particle being measured with the use of a semi-empirical formula based on calibration with spheres of known diameters (Herman 1992; Herman et al. 2004, 2006). For data acquisition, field measurements control and pre-processing software provided by Rolls-Royce Naval Marine

Canada (formerly ODIM Brooke Ocean) was used. Extensive post-processing filtering and interpretation in several steps was implemented on the raw LOPC data. A group of particles corresponding to the size of copepodite stages of *Calanus* spp. 1.0-2.5 mm ESD was selected and its percentage was shown in the total abundance of mesozooplankton community (0.25 – 5 mm ESD). Particles <0.25 were excluded from analysis since they are considered to be a noise (Zhou et al. 2009; Basedow et al. 2010). To count higher level parameters post-processing tools written in Matlab were developed. To calculate the abundance of plankton expressed as the number of individuals per cubic meter (ind. m<sup>-3</sup>) the recorded count data and flow data were used.

## **2.3. LABORATORY ANALYSES**

### **Net samples**

Detailed laboratory analyses of each sample was performed according to a standard procedure of Kwasniewski et al. (2010). First, zooplankters larger than 0.5 cm were picked out from the sample, identified and counted. After that, 2 ml subsamples were taken out from each sample with a macropipette according to sub-sampling method by Harris et al. (2000). Subsamples were taken out successively until at least 400 individuals were counted in a single sample. All organisms in subsamples were identified to the lowest possible taxonomic level, typically species, under microscope. The special focus was put on *Calanus* spp. and its copepodite stages which were identified according to criteria described by Kwasniewski et al. (2003). The abbreviations (CI-AF) used in the work refer to successive copepodite stages of *Calanus* spp. CI, CII, CIII, CIV and CV are the first five copepodite stages, AF (adult females), is the sixth copepodite stage. After microscope analysis the number of individuals in each sample was converted into abundance (ind. m<sup>-3</sup>). This was done on the basis of filtered water volume. Zooplankton dry mass was calculated according to Kwasniewski et al. (2010).

### ***Calanus* spp. body size measurements**

For all copepodite stages of *C. glacialis* and *C. finmarchicus* the measurements of the prosome length were performed until at least 30 individuals from each copepodite stage in the subsamples were counted. In order to compare the prosome length of all *Calanus*



spp. copepodite stages the prosome length of 11 388 individuals was measured. Among them there were 1330 CI, 1742 CII, 2604 CII, 3181 CIV, 2345 CV and 185 AF individuals. To compare prosome length of the fifth *Calanus* spp. copepodite stage (CV) 1 575 individuals from Hornsund and 785 from Kongsfjorden were analysed. The number of all CVs in the sample (ind. m<sup>-3</sup>) from both *C. glacialis* and *C. finmarchicus* was divided by the total number of measured organisms in the sample. To determine the relative abundance of measured individuals in the sample each measurement of a given individual was multiplied by the factor: abundance of CV (ind. m<sup>-3</sup>) / number of measured individuals. Measured individuals were classified into size classes every 0.05 mm.

### **Diet samples**

Similarly to net samples all diet samples were subjected to qualitative and quantitative analysis following the standard procedure described by Kwasniewski et al. (2010). Instead of abundance, the dry mass calculated according to Kwasniewski et al. (2010) is given in all the results, since the importance of diet components is related primarily to the amount of energy they can provide.

## **2.4. STATISTICAL ANALYSES**

The multivariate nonparametric permutational ANOVA (PERMANOVA; Anderson et al. 2008) was used to test the differences in: *Calanus* spp. prosome length of all the copepodite stages of; zooplankton community structure; *Calanus* spp. copepodite structure; copepodite stage index; percentage of *Calanus* spp. CV biomass in total zooplankton biomass (TZB); diet composition; and *Calanus* spp. older copepodite stages composition. In all the analyses factors were fixed. Prior to the analyses data were square-root-transformed (Clarke and Gorley 2001). The distribution of samples was illustrated with a non-metric multi-dimensional scaling (nMDS) using Bray-Curtis similarities ordinations. The calculation of the Pseudo-F and p values was based on 999 permutations of the residuals under a reduced model (Anderson and Ter Braak 2003). Bold in tables with PERMANOVA results s means p<0.05, df are degrees of freedom, MS represents means of squares,  $\sqrt{ECV}$  are square root of the estimated components of variance. Relationship between the *Calanus* spp. prosome length and seawater temperature was tested with the use of Pearson linear correlation.

To determine the zooplankton community structure the relative abundance of species/taxa was used. For each study period, the median number of individuals of given taxa was calculated. Taxa constituting more than 5% of the total zooplankton abundance were distinguished, the rest was grouped into the “others” category. Due to logistic constraints resulting in different sampling frequency and different nets in Kongsfjorden only K1 and K1’ could be compared.

To test the differences in copepodite structure between Kongsfjorden and Hornsund, *Calanus* spp. copepodite stages percentages from corresponding study periods were compared (i.e. H3 with K3 in 2015 and H2’ with K1.5’ in 2016). The *Calanus* spp. stage index was calculated as mean stage weighted on the basis of relative abundance. Each stages were given values from 1 (CI) to 6 (CVI) (Kwasniewski et al. 2012), where CVI stage was represented only by adult females.

A distance-based linear model (DistLM) was used to analyse the relationships between the distribution of *Calanus* spp. fraction and the environmental variables. Relative *Calanus* spp. fraction abundances were normalized before the analysis. A forward-selection procedure was used to determine the best combination of predictor variables explaining variations in *Calanus* spp. distribution. The selection criteria were based on  $R^2$  values (Anderson et al. 2008). Distance-based redundancy (dbRDA) plots were used to illustrate DistLM results of relationship between *Calanus* spp. distribution and environmental variables.

Diet composition of little auk chicks’ was visualized with zooplankton biomass data. Taxa constituting more than 5% of the total zooplankton abundance were distinguished, the rest was grouped into the “others” category. A similarity percentages (SIMPER) analysis was used to determine the contribution of zooplankton taxa present in the little auks diet. Only taxa contributing >5% for dissimilarities were listed.

When comparing diet samples with seawater zooplankton samples only *Calanus* spp. copepodite structure were taken into consideration. The *Calanus* spp. older copepodite stages CIV-AF biomass percentage in the little auk diet samples was compared with seawater zooplankton samples between the corresponding study periods in in Hornsund (H2a vs. Hc1, H2b vs. Hc2, H3 vs. Hc3, H2’ vs. Hc3’ and in Kongsfjorden: K1 vs. Kc1a, K2 vs. Kc2b, K1’ vs. Kc1’a, K1.5’ vs. Kc1’b, in two years (2015, 2016)

Statistical tests were performed in PRIMER 7/PERMANOVA+ and Statistica 13.1 (StatSoft). Maps illustrating temperature, salinity, chlorophyll fluorescence and *Calanus*



spp. availability were prepared using Ocean Data View 5.1.2 software (Schlitzer 2018) and DIVA interpolation was used.

### **Model assumptions**

In order to estimate changes in the age structure of the two potential *Calanus* species representing different reproductive strategies, their population development rates and life history strategies were modeled in response to various temperature regimes. To cover a wide range of possible cases and scenarios the following, described below, parameters and assumptions were established and incorporated into the model.

#### *Seawater temperature*

Two scenarios assuming different temperature conditions were adopted. The first scenario was assuming a constant temperature of 3°C, which is considered more optimal for the development of *C. glacialis* than *C. finmarchicus* (Campbell et al. 2001; Daase et al. 2011; Grenvald et al. 2013). The second scenario was assuming higher temperature of 6°C, which is the upper temperature tolerance for *C. glacialis* (Carstensen et al. 2012; Pasternak et al. 2013; Alcaraz et al. 2014). July 3<sup>rd</sup> an in-situ data collection starting point in 2015 - was set as the model start date. Then the two consecutive study periods of summer season were determined at a time interval of 20 days (23<sup>rd</sup> July and 12<sup>th</sup> August) similarly to the study periods of zooplankton sampling.

#### *Calanus age structure at the starting point*

Initial abundance of individuals in each developmental stages was equaling abundance of individuals in samples collected at the beginning of July 2015 (in H1) and was the same for both species. The year 2015 was chosen as the reference point as in H1 and H2 the same stable seawater temperature of 3°C was recorded. In addition to the copepodite stages, the abundance of the naupliar stages (N3-N6) was also included to the starting point of the model. N3 was chosen as the first feeding nauplius stage for *C. glacialis*, while N1-N6 for *C. finmarchicus*. Several generations were presumed during one season (Madsen et al. 2001, Daase et al. 2013). It was assumed also that at the beginning of July late nauplii stages will dominate in *C. glacialis* since N3 stage can be reached just 6-7 weeks after egg production (Ji et al. 2012), which takes place during spring bloom. For

*C. glacialis* The abundance of each nauplii stage (N3-N6) was 1/4 of the average copepod nauplii abundance calculated in H1 period in 2015 and for *C. finmarchicus* 1/6 for N1-N6.

### *Different reproductive strategies*

Since both *Calanus* species represent different reproductive strategies; i.e. *C. glacialis* usually completes its life cycle in 2 years and *C. finmarchicus* can produce several generations during one season (Madsen et al. 2001, Daase et al. 2013), the model assumes that *C. glacialis* will not produce eggs from the beginning of July to mid-August, while *C. finmarchicus* will reproduce throughout the period. Similarly to Ji (2012) sex ratio was equal, where half of the CVs will become adult females. The ratio of mature to immature females of *C. finmarchicus* depends on the food availability and can range from a just few to over 80% during the season (Niehoff et al. 1999). The model did not take into account the phytoplankton production cycle (Niehoff et al. 1999) thus an average of 50% mature females, ready to produce eggs, was incorporated into the model.

### *Egg production*

*Calanus finmarchicus* egg production rate was adopted from Hirche et al. (1997). Since egg production rate increase with temperature (Hirche et al. 1997; Pasternak et al. 2013) different coefficients were used in the two scenarios. In a 3°C scenario 31 eggs female<sup>-1</sup> d<sup>-1</sup> was assumed as an average of minimum egg production in 2°C and 5°C. In the 6°C scenario an average of minimum egg production in 5°C and 8°C was adopted in the rate of 47 eggs female<sup>-1</sup> d<sup>-1</sup>. Additionally 2 day spawning interval was assumed for *C. finmarchicus* females in 3°C scenario and every day spawning in 6°C scenario. This was based on an average egg production rate for temperatures 2°C and 5°C (Hirche et al. 1997) for the first scenario and 5°C and 8°C (Hirche et al. 1997) for the second scenario.

### *Mortality*

Species – and copepodite-specific mortality rates were applied in accordance with Arnkværn et al. (2005), for *C. glacialis*: CI 0.002 d<sup>-1</sup>; CII 0.004 d<sup>-1</sup>; CIII 0.016 d<sup>-1</sup>; CIV 0.033 d<sup>-1</sup>; CV 0.075 d<sup>-1</sup>; AF 0.049 d<sup>-1</sup> and for *C. finmarchicus*: CI 0.026 d<sup>-1</sup>; CII 0.034 d<sup>-1</sup>; CIII 0.04 d<sup>-1</sup>; CIV 0.045 d<sup>-1</sup>; CV 0.09 d<sup>-1</sup>; AF 0.0 d<sup>-1</sup>. For nauplii and for eggs the mortality rate was assumed as 0.04 d<sup>-1</sup> for eggs and 0.07 d<sup>-1</sup> for the three nauplii stages (Ji 2011).

### *Development rates*

In order to determine the development rates of *C. glacialis* and *C. finmarchicus* the commonly used function of Corkett et al. (1986) was used. The development time ( $D$ ) of each stage was determined using the equation:

$$D = a(T + \alpha)^\beta$$

where  $D$  is development time in days,  $a$ ,  $\alpha$  and  $\beta$  are fitted constants, and  $T$  is ambient temperature ( $^{\circ}\text{C}$ ). The value  $\beta = -2.05$  is the mean for 11 species of copepods (Corkett et al. 1986). Both  $\beta$  and  $\alpha$  were found to be constant throughout the life span (Corkett et al. 1986). The value for  $\alpha$  is different for *C. glacialis* and *C. finmarchicus* and is equal to 13.04 and 9.11, respectively. The stage specific development time  $a$  values, different for *C. glacialis* and *C. finmarchicus*, were applied following calculations of Ji et al. (2012), where  $a$  value was based on the equiproportional rule for the development of copepods described by Hart (1990).

### *Diapause*

The diapause coefficient has been set based on the fraction of CVs in diapause for each day of the year demonstrated by Fiksen (2000). Because in the literature there is no accurate data on exact timing and extent of the population of *C. glacialis* that falls into diapause, the assumptions regarding the timing of diapause for *C. finmarchicus* (Fiksen 2000) were adopted for both species.

### 3. RESULTS

#### 3.1. *CALANUS* SPP. SIZE SPECTRA IN FORAGING GROUNDS OF LITTLE AUKS

##### 3.1.1. ALL COPEPODITE STAGES OF *CALANUS* SPP.

The prosome length of *Calanus* spp. copepodite stages differed significantly between the two fjords for CI-CV, while it was similar for CVI (adult females – AF; Table 3). In general the median prosome length of *Calanus* spp. individuals was larger in Hornsund than in Kongsfjorden (Fig. 4). The size range of *Calanus* spp. individuals ranged from 0.5 mm for CI to 4.3 mm for CVI (AF).

Table 3. Results of one-factor multivariate PERMANOVA for the prosome length of *Calanus* spp. copepodite stages in Hornsund and Kongsfjorden.

Copepodite stage	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
CI	Fjord	1	1274.8	212.98	<b>0.001</b>	1.40
CII	Fjord	1	5180.9	560.51	<b>0.001</b>	2.43
CIII	Fjord	1	8748.4	1086.40	<b>0.001</b>	2.74
CIV	Fjord	1	5728.8	720.28	<b>0.001</b>	1.98
CV	Fjord	1	2277.5	237.43	<b>0.001</b>	1.43
CVI (AF)	Fjord	1	1.2	0.22	0.630	-0.18

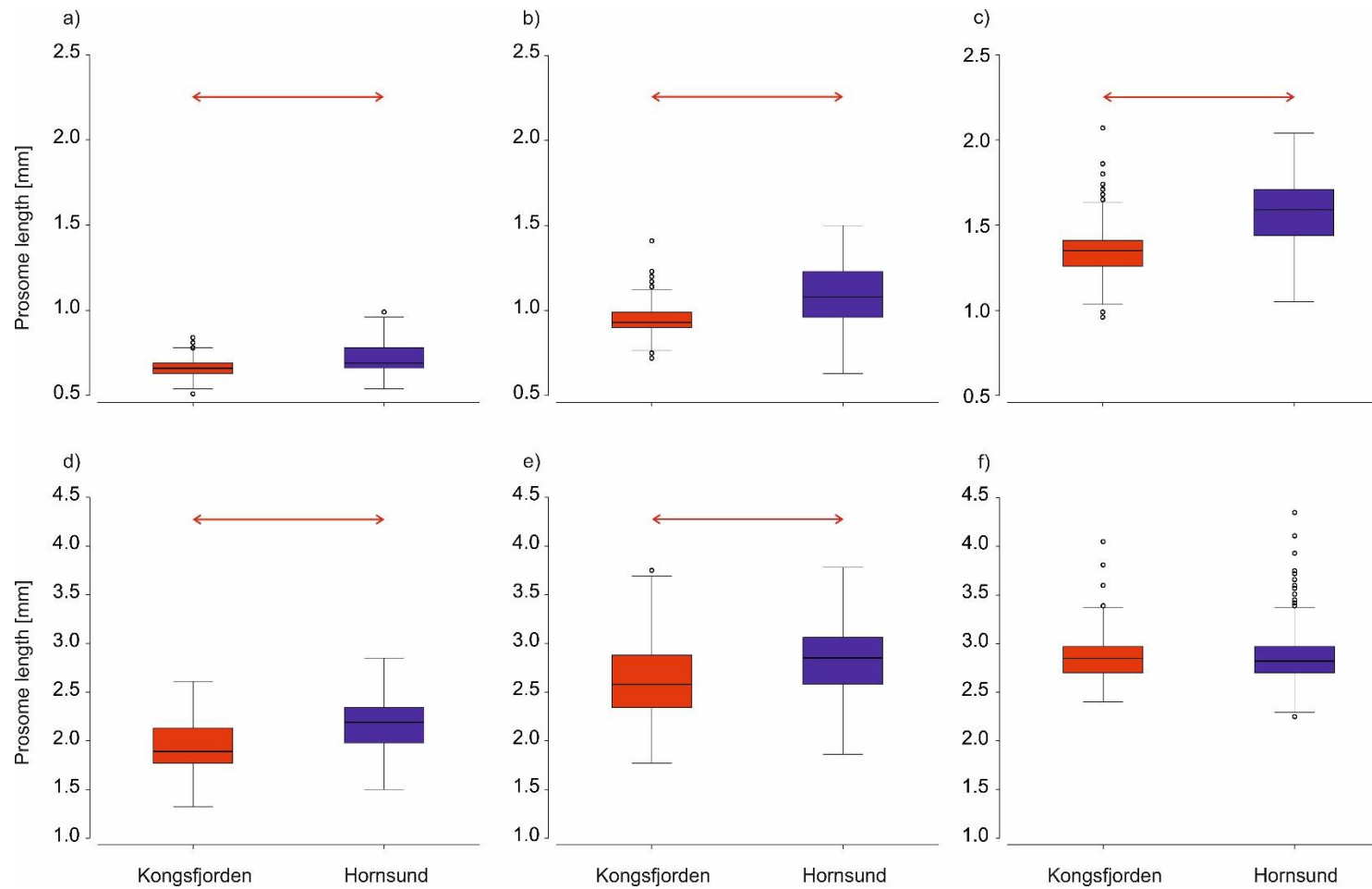


Fig. 4. Prosome length of *Calanus* spp. copepodite stages: CI (a), CII (b), CIII (c), CIV (d), CV (e) and CVI (AF) (f) in Kongsfjorden and Hornsund. Horizontal black lines shows the median, box represents percentiles, whiskers ranges, dots are values outside the range, red arrows shows statistically significant differences.

### 3.1.2. FIFTH COPEPODITE STAGE OF *CALANUS* SPP.

#### Hornsund

Among the fifth copepodite - CV individuals the smallest size class had the prosome length of 1.8-1.9 mm, while the largest of 3.7-3.8 mm (Fig. 5). The most common were individuals with prosome length of 2.4-2.5 mm, classified as *Calanus finmarchicus*, according to morphological classification based on prosome length (Kwasniewski et al. 2003). Individuals larger than 2.9 mm classified as *Calanus glacialis* were less numerous. Generally, three main size classes of *Calanus* spp. CV were observed 2.4-2.5 mm, 2.7-2.8 mm and 2.9-3.0 mm. Such a size distribution, does not have the features of normal distribution. In the case of size range related to *C. finmarchicus*, two distinct peaks can be determined on the basis of the data distribution. Yet, they did not overlap with the normal distribution curve fitted for these data. In the case of the *C. glacialis*, the same situation occurs. Its size distribution is right-skewed with the highest number of individuals at the lower size limit of the species range, which also did not overlap with normal distribution curve fitted. Additionally, normal distributions curves for both species clearly overlap in size range between 2.6 and 3.2 mm.

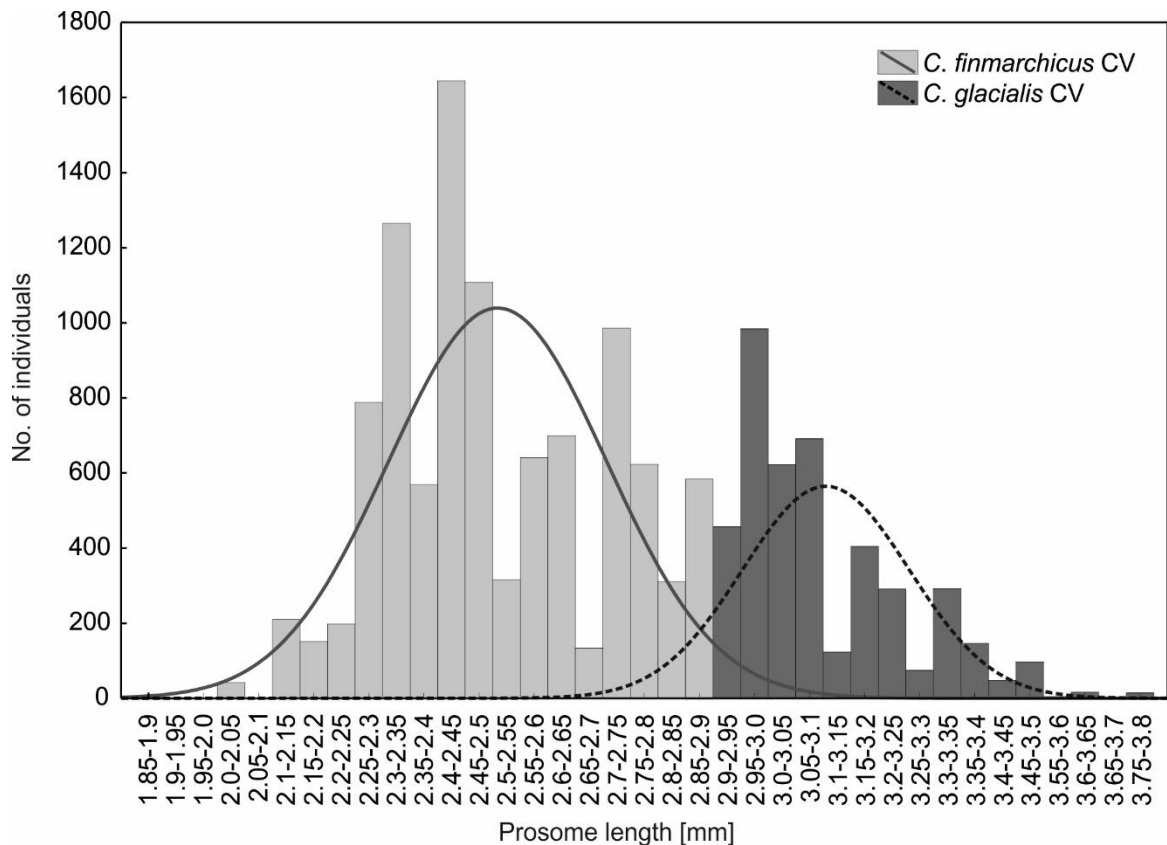


Fig. 5. Distribution of *C. finmarchicus* and *C. glacialis* fifth copepodite stage (CV) prosome length in Hornsund based on morphological identification. Solid and dotted lines indicate normal distributions.

### Kongsfjorden

Similarly to Hornsund, individuals between 2.4 and 2.5 mm size of prosome length corresponding to *C. finmarchicus* size range (according to Kwasniewski et al. 2003), were the most numerous among the *Calanus* spp. CV individuals found in Kongsfjorden (Fig. 6). However the peak was not that distinct, as the abundance of organisms within a wider size range of 2.0-2.8 mm remained at relatively high and similar level. Within the size range corresponding to *C. glacialis* (according to Kwasniewski et al. 2003), the most numerous were individuals of the 3.0-3.1 mm prosome length. The size distribution for both species classified according to morphological characteristic differs from the typical normal distribution curves determined for these data. Moreover, the normal distributions curves for both species clearly overlap.

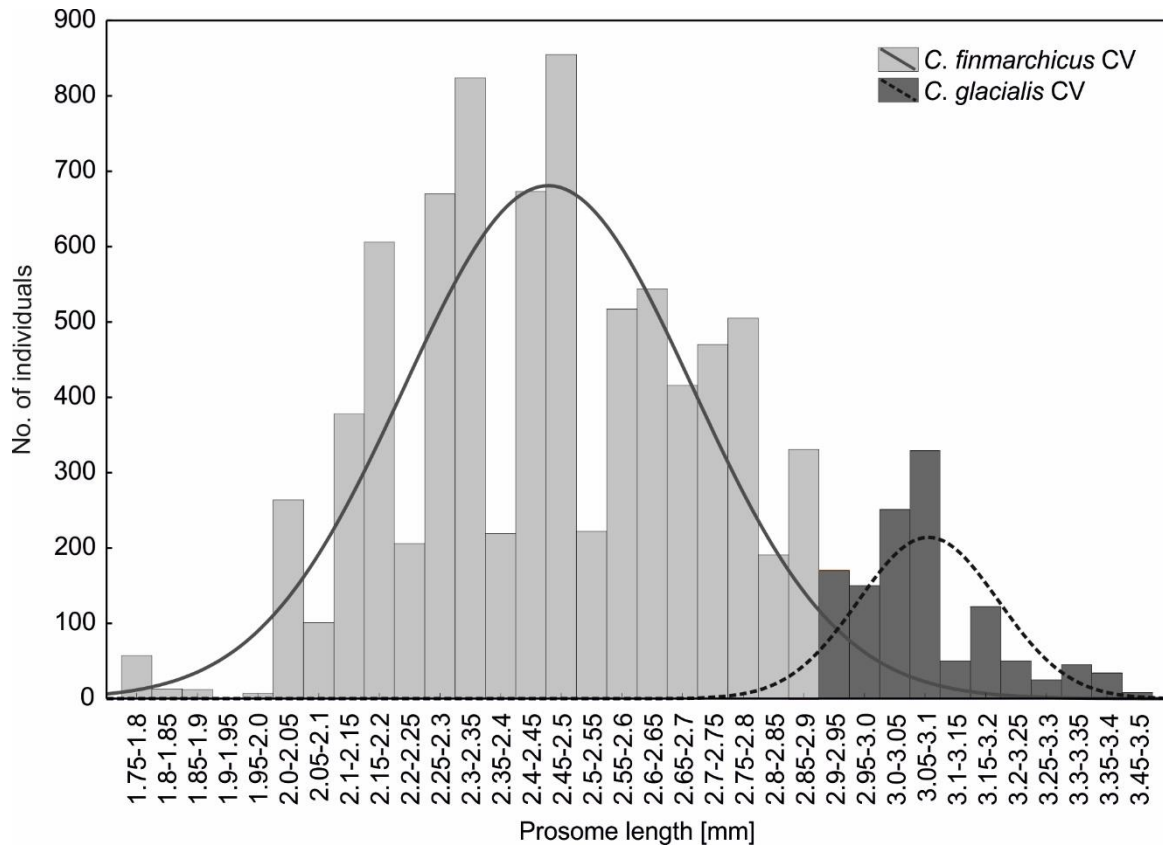


Fig. 6. Distribution of *C. finmarchicus* and *C. glacialis* fifth copepodite stage (CV) prosome length in Kongsfjorden based on morphological identification. Solid and dotted lines indicate normal distributions.

Results from both fjords show a clear separation of both species identified only on the basis of morphometric measurements (Figs. 5, 6). Recent molecular research (Choquet et al. 2018, Renaud et al. 2018) also questioned the morphometric measurement method for identification. Therefore in this dissertation both sibling species (*C. glacialis* and *C. finmarchicus*) were combined into one *Calanus* spp. group.

### 3.1.3. RELATIONSHIP BETWEEN PROSOME LENGTH OF *CALANUS* SPP. COPEPODITE STAGES AND SEAWATER TEMPERATURE

The prosome length tend to decrease with increasing temperature in both fjords (Fig. 7). The Pearson Correlation Coefficient showed a weak, but significant, negative linear relationship ( $R = -0.39$   $p < 0.0001$ ). Generally, there was a relatively large variation in the body size of *Calanus* spp. CV individuals. Their prosome length ranged from 1.8 to 3.8



mm. The largest individuals were observed at a temperature of 2-4°C. At temperature exceeding 7°C there were no individuals with longer prosome length than 2.8 mm.

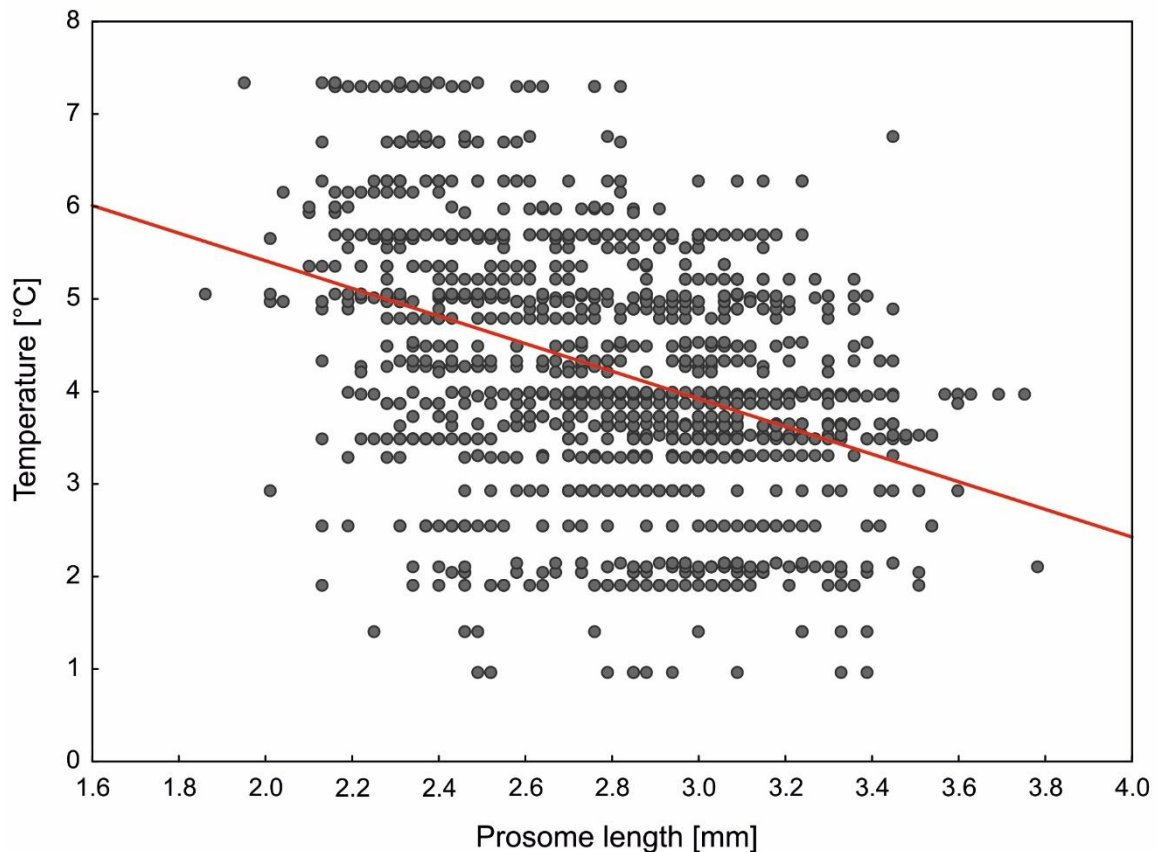


Fig. 7. Prosome length of *Calanus* spp. copepodite stages and seawater temperature relationship. Dots represent single individual measured in both fjords. Trendline is marked in red.

## 3.2. CALANUS SPP. IN ZOOPLANKTON COMMUNITY

### 3.2.1. ZOOPLANKTON COMMUNITY STRUCTURE

#### Hornsund

The zooplankton community structure differed between the two years and between study periods in Hornsund (Table 4). In 2015, the zooplankton community was dominated by *Calanus* spp., which constituted about 60% of total zooplankton abundance in all three study periods. The second most numerous taxon was *Oithona similis* with 20% of total

zooplankton abundance throughout the season (Fig. 8a). Copepoda nauplii constituted also a significant percentage in the total zooplankton abundance since they comprised almost 20% in H1. Their number was lower (less than 3%) in H3. *Pseudocalanus* spp. represented the opposite trend. Their contribution increased from almost 5% in H1 to 10% in H2 and H3. The mean size of zooplankton organisms also changed over time from about 840  $\mu\text{m}$  in H1 to up to 1636  $\mu\text{m}$  in H3.

In 2016 the percentage of *Calanus* spp. in total zooplankton abundance remained at approximately 40%, in all study periods (Fig. 8b). High percentage of *O. similis* in total zooplankton abundance was also observed. It raised from over 20% in H1' to almost 40% in H3'. *Pseudocalanus* spp. was most abundant in H2' with over 20% of overall zooplankton community. The highest abundance of Copepoda nauplii was observed in H1', when it constituted almost 20% of total zooplankton abundance. Bivalvia veligers, which comprised about 10% of all taxa in H2' and H3', were another numerically important taxa. The mean size of zooplankton organisms in 2016 in Hornsund remained at a similar level (~1000  $\mu\text{m}$ ) in all studied periods.

Table 4. Results of two-factor multivariate PERMANOVA for the zooplankton community structure in Hornsund.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Year	1	3245.0	5.83	<b>0.001</b>	11.99	
Period	2	5222.6	9.39	<b>0.001</b>	18.09	
						2015: H1 $\neq$ H3; H2 $\neq$ H3
Year x Period	2	1661.3	2.98	<b>0.003</b>	12.45	2016: H1' $\neq$ H2'; H1' $\neq$ H3'; H2' $\neq$ H3'

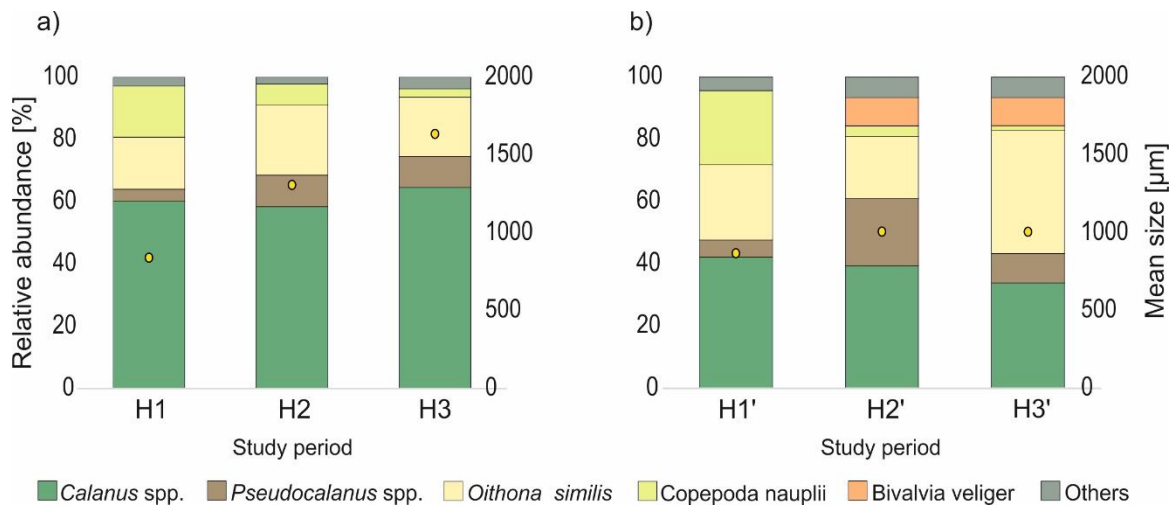


Fig. 8. Zooplankton community structure and mean size of zooplankton individuals (marked as yellow dots) in Hornsund in 2015 (a) and 2016 (b).

### Kongsfjorden

Zooplankton community structure in Kongsfjorden was significantly different between the two years (Table 5) and study periods (Table 6). In K2 samples were collected with different net which excluded them from the current analysis (see M&M for details). In 2015 *Calanus* spp. was the most abundant taxa in K1, when it reached 47% of the total zooplankton abundance. Its percentage decreased to 25% in K3 (Fig. 9a). The second numerous taxon was *O. similis* with approximately 30% in K1 and 46% in K3. Copepoda nauplii in both study periods constituted less than 1% of the zooplankton abundance. The percentage of *Bivalvia* veligers was relatively low with values below 1% in K1 to approximately 5% in K3. The mean size of all zooplankton individuals was approximately 1000 µm in both study periods.

In 2016 *Calanus* spp. percentage was relatively low, and decreased from 12% in K1' and K1.5' to 5% in K2' (Fig. 9b). More numerous were: *O. similis* with about 20% throughout three study periods, *Bivalvia* veligers with percentage ranging from 17 to 26%, and *Limacina helicina* with fluctuating from 16 to 31% contribution. The percentage of *Pseudocalanus* spp. and Copepoda nauplii remained relatively low during whole study season, never exceeding 10% each. The mean size of all zooplankton organisms in Kongsfjorden was relatively small and constant in 2016 reaching approximately 500 µm.

Table 5. Results of one-factor multivariate PERMANOVA for the zooplankton community structure in Kongsfjorden with year as a factor.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Year	1	6127.4	16.13	<b>0.001</b>	25.27

Table 6. Results of one-factor multivariate PERMANOVA for the zooplankton community structure in Kongsfjorden with study period as a factor.

Year	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
2015	Period	1	1776.3	5.22	<b>0.003</b>	14.12	
2016	Period	1	2133.0	4.49	<b>0.001</b>	13.84	K1'≠K2'; K1.5'≠K2'

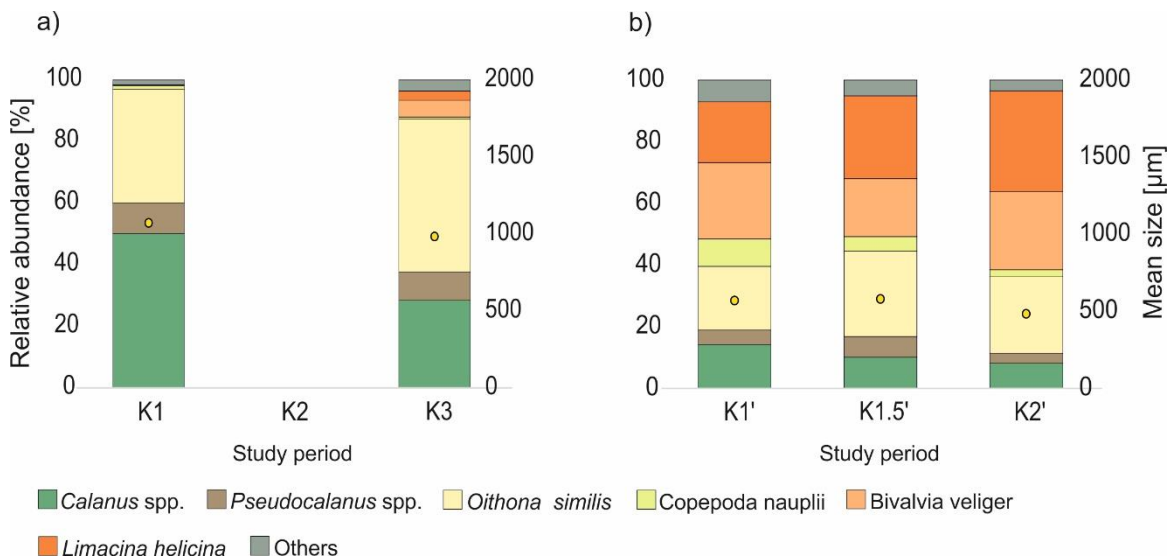


Fig. 9. Zooplankton community structure and mean size of zooplankton individuals (marked as yellow dots) in Kongsfjorden in 2015 (a) and 2016 (b).

### Hornsund vs. Kongsfjorden

The zooplankton community structure differed significantly between the two fjords in two years (Table 7) which is clearly visible on the nMDS plot, by separation of the samples from different study periods (Fig. 10). SIMPER analysis indicated that the average dissimilarity between H3 and K3 periods was relatively high (49%), and was influenced mostly by *O. similis* (24%), *Calanus* spp. AF (13%) and *Bivalvia veliger* (11%) (Fig. 11a). The average dissimilarity between H2' and K1.5' periods was only slightly lower (41%)

with *L. helicina* veliger (18%), *Bivalvia* veliger (14%), *O. similis* (11%) and *Calanus* spp. (10%) responsible the most for the observed differences (Fig. 11b).

Table 7. Results of two-factor multivariate PERMANOVA for the zooplankton community structure in Kongsfjorden and Hornsund.

Year	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
2015	Fjord	1	5780.2	14.95	<b>0.004</b>	28.89
2016	Fjord	1	4467.4	9.35	<b>0.001</b>	19.55

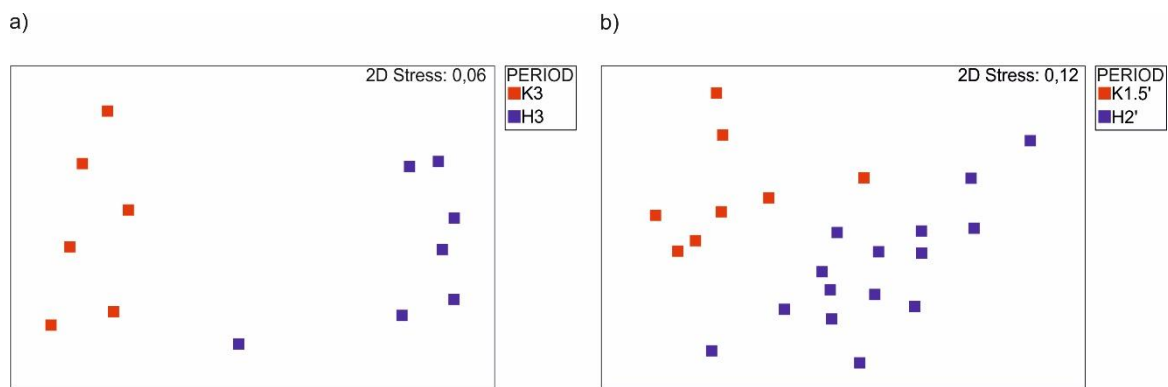


Fig. 10. The nMDS of the zooplankton community structure at particular stations in Kongsfjorden (red) and Hornsund (blue) in: 2015 (a) and 2016 (b).

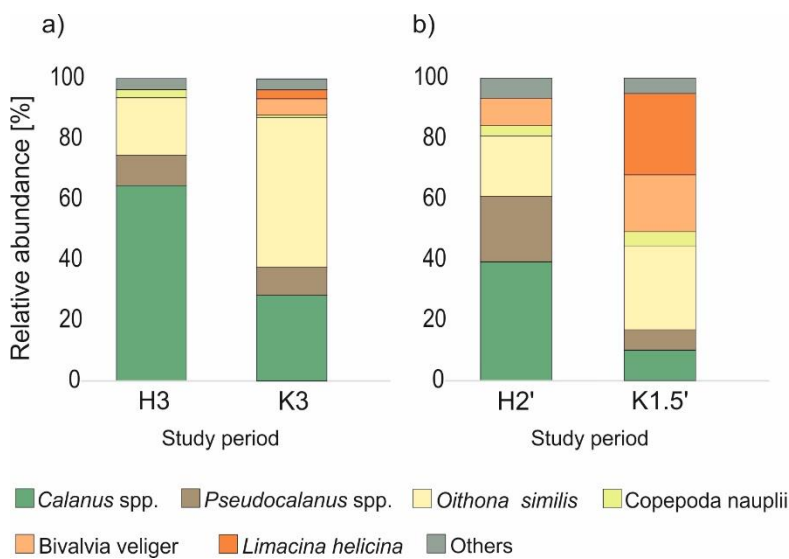


Fig. 11. Comparison of zooplankton community structure in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b).

### 3.2.2. RELATIONSHIP BETWEEN MEAN ORGANISM SIZE OF ZOOPLANKTON AND SEAWATER TEMPERATURE

A significant negative correlation between the mean zooplankton organism body size and seawater temperature was observed (samples from both fjords combined, Pearson's correlation  $R = -0.46$ ;  $p = 0.001$ ; Fig. 12). The larger organisms ( $>1200 \mu\text{m}$ ) were indicated mainly in lower seawater temperatures, i.e. below  $4^\circ\text{C}$ .

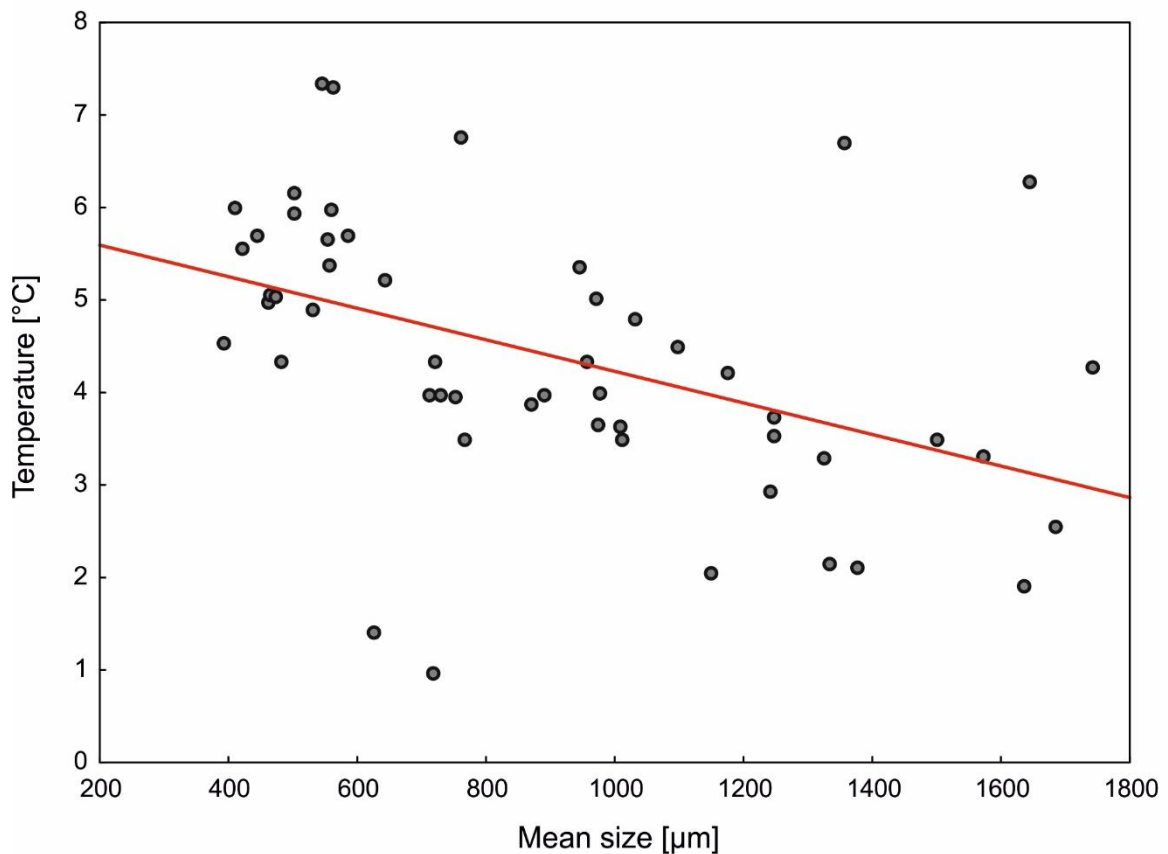


Fig. 12. Relationship between the mean size of zooplankton individuals and seawater temperature. Each dot represents mean size in particular sample. Trendline is marked in red.

### 3.3. CALANUS SPP. PHENOLOGY

#### 3.3.1. CALANUS SPP. COPEPODITE STRUCTURE

##### Hornsund

##### *Percentage*

The copepodite structure of *Calanus* spp. differed between years and study periods (Table 8, Fig. 13). The overall spread of distances between the points representing periods of sample collection indicated that the percentages of *Calanus* spp. copepodite stages were much more similar within corresponding study periods (for example H1 and H1'), than between individual periods within one year (for example H1 and H2). All the periods differed significantly from each other in terms of the percentage of copepodite stages (PERMANOVA post hoc Table 8).

Table 8. Results of two-factor multivariate PERMANOVA for the *Calanus* spp. copepodite structure in Hornsund.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Year	1	475.1	3.98	<b>0.026</b>	4.36
Period	2	3724.2	31.16	<b>0.001</b>	15.90
Year x Period	2	147.2	1.23	0.290	1.97

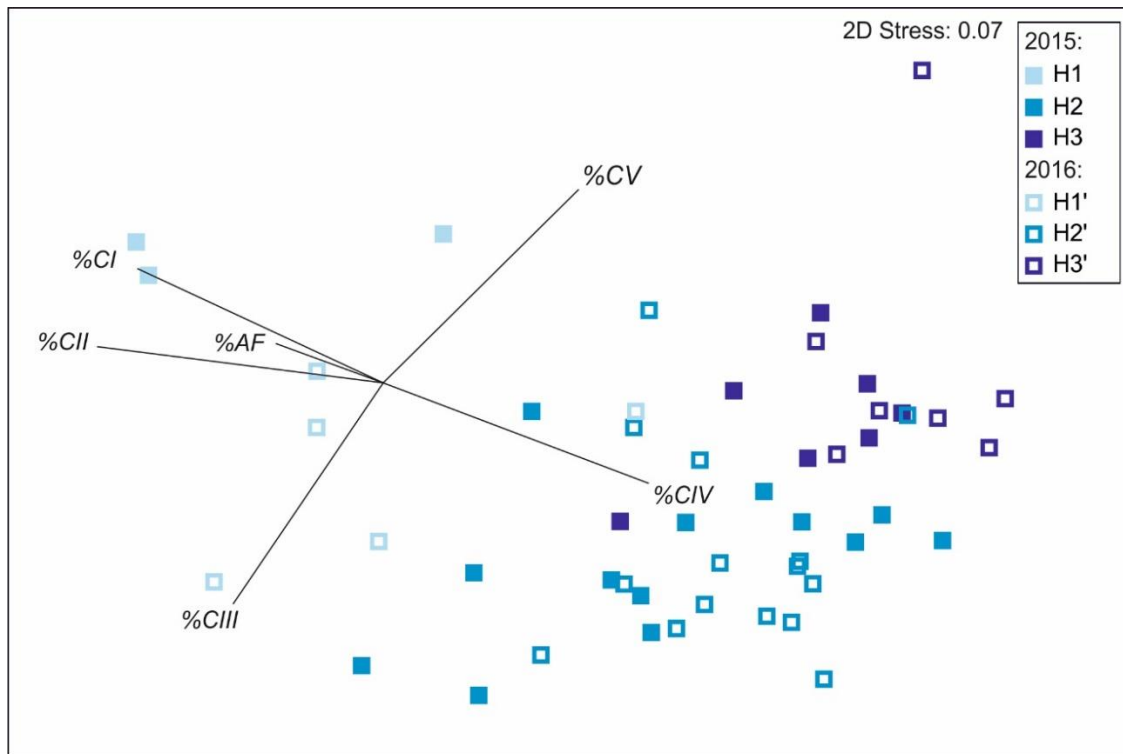


Fig. 13. The nMDS of the *Calanus* spp. copepodite structure in Hornsund. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

Differences in copepodite structure among various study periods in both years had a gradual character (Fig. 14a, b). Although the highest percentages of the earliest copepodites of *Calanus* spp. (CI and CII) were observed in both years in the same, early period (H1 and H1'), their combined percentage was almost two times higher in 2015 than in 2016. Thus, the correlation of these stages with the ordination coordinates was stronger concerning samples from 2015 (Fig. 13). The highest percentages of CIII were observed in H2 (31%) and in both H1' and H2' (25%). In turn, the highest percentages of CIV were observed in H2 and H3 with slightly higher values in 2016 during H2' and H3'. The peak occurrence of CV took place in H3 and H3'. The percentage of AF was relatively minor but slightly higher values were indicated in the first study period in both years.



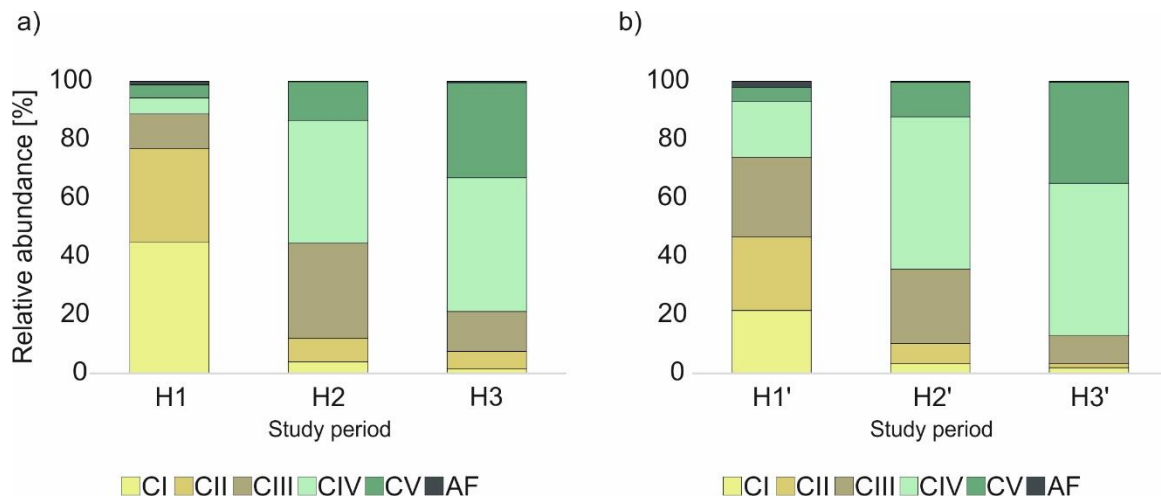


Fig. 14. *Calanus* spp. copepodite structure in Hornsund in 2015 (a) and 2016 (b).

### Abundance

Early *Calanus* spp. copepodite stages (CI-CIII) generally, were more abundant in 2015 than in 2016. The highest abundances of older copepodite stages CIV and CV were observed in 2016 (Table 9). CIV was the most abundant copepodite stage in this study in Hornsund. The abundance of AF was relatively low except for distinct peak in abundance in H1 despite its higher percentage in H1'.

### Biomass

The early copepodite stages CI-CIII had relatively low biomass in both years, with slightly higher values in 2015 (Table 9). The biomass of CIV was the highest in comparison to the other *Calanus* spp. stages in both study years. Similarly to the earliest copepodite stages, the biomass of AF was relatively low throughout the study periods in both years.

Table 9. Abundance (ind. m<sup>-3</sup>) and biomass (g m<sup>-3</sup>) of *Calanus* spp. copepodite stages (CI-AF) from Hornsund. *M* median, *Q*<sub>1</sub>-*Q*<sub>3</sub> percentiles 25-75%, *N* number of samples.

Study Period		<i>Calanus</i> spp. copepodite stage													
		CI		CII		CIII		CIV		CV		AF		<i>N</i>	
		<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>		
Abundance	2015	H1	312.0	126.9-1232.0	212.0	85.3-872.0	144.0	30.9-392.0	152.0	11.7-208.0	80.0	11.7-220.0	34.6	1.4-129.3	3
		H2	70.0	36.0-104.0	155.0	108.0-240.0	438.0	330.0-785.0	564.0	343.3-1936.0	170.0	86.7-656.0	2.6	1.7-5.3	13
		H3	10.7	6.0-13.5	34.5	24.0-5.0	103.3	44.0-224.0	248.0	178.0-440.0	224.0	140.0-297.5	3.5	2.0-8.2	7
	2016	H1'	76.5	38.0-127.0	93.0	58.0-102.0	96.0	87.0-109.0	62.0	54.0-76.0	19.0	11.0-38.0	6.0	5.0-7.5	5
		H2'	60.0	26.7-92.0	120.0	44.0-241.8	442.7	244.0-736.0	757.3	404.0-1480.0	218.7	90.7-353.3	7.1	4.0-14.2	15
		H3'	8.0	2.7-14.0	9.3	5.3-15.0	42.0	6.7-60.0	160.0	37.3-624.0	315.0	24.0-440.0	4.0	0.0-8.0	7
Biomass	2015	H1	2.2	0.9-8.0	3.4	1.7-12.0	7.0	1.7-14.4	15.3	1.8-32.3	20.4	4.2-86.0	1.7	0.4-3.5	3
		H2	0.4	0.2-0.6	2.4	1.6-3.1	21.8	14.2-37.9	90.5	42.8-180.8	72.9	36.1-205.3	0.0	0.0-1.7	13
		H3	0.1	0.0-0.1	0.7	0.4-1.0	5.0	2.3-10.8	30.6	22.2-54.5	77.2	50.9-170.2	2.6	0.9-4.6	7
	2016	H1'	0.5	0.3-0.7	1.3	1.1-1.5	4.8	4.6-5.3	10.8	9.6-11.8	11.4	6.4-21.5	1.3	1.3-2.0	5
		H2'	0.3	0.1-0.5	1.4	0.6-2.7	21.8	9.6-31.4	93.8	49.0-170.6	70.6	23.7-97.2	2.3	0.4-4.6	15
		H3'	0.0	0.0-0.1	0.1	0.1-0.2	1.3	0.2-1.8	20.3	4.0-78.1	86.9	7.3-160.0	0.0	0.0-1.7	7

## Kongsfjorden

### Percentage

The copepodite structure of *Calanus* spp. differed between the years and study periods (Table 10, Fig. 15) which was shown by the overall spread of distances between the points representing periods of sample collection. Differences between the study periods (K1≠K2) were found only in 2015 (PERMANOVA post hoc Table 10).

Table 10. Results of two-factor multivariate PERMANOVA for the *Calanus* spp. copepodite structure in Kongsfjorden.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Year	1	6079.7	15.19	<b>0.001</b>	19.46	
Period	2	2157.9	5.39	<b>0.007</b>	10.82	
Year x Period	2	1782.3	4.45	<b>0.013</b>	20.00	2015: K1≠K2

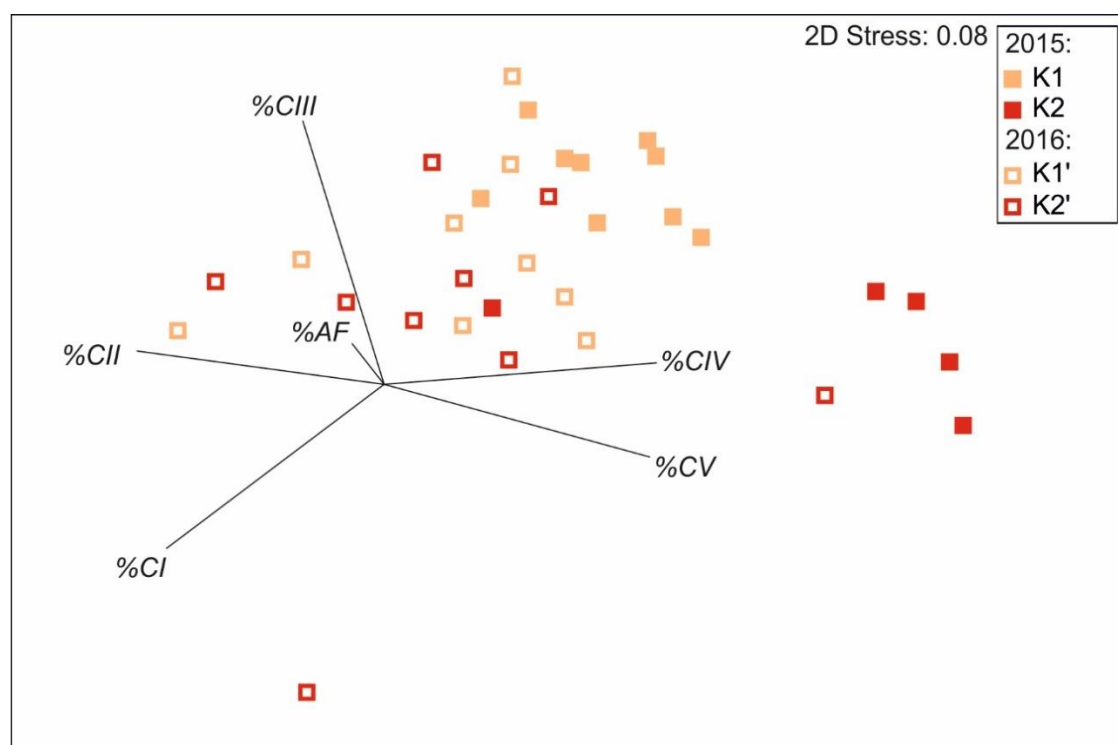


Fig. 15. The nMDS of the *Calanus* spp. copepodite structure in Kongsfjorden. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

Large differences in copepodite structure were observed only in 2015 when the percentage of early copepodite stages (CI-CIII) decreased from over 50% in K1 to about 10% in K3 (Fig. 16a). Within the early stages (CI-CIII) of the *Calanus* spp. in 2015, the percentage of CIII was always the highest. The peak in the percentage of CIV was observed in K2, while the percentage of CV increased gradually to approximately 50% in K3. The percentage of AF was very small with a slightly higher value not exceeding 2% in K1.

In 2016, the percentage of all *Calanus* spp. copepodite stages was very similar in all study periods (Fig. 16b). The CI-CIII constituted approximately 60% of all copepodite stages with about 20% share for each stage. The percentage of late stages was also quite similar with slightly higher values of CIV in K1' and higher contribution of CV in K2'. The percentage of AF was slightly higher in K1' and K2', however, generally it did not exceed 2%.

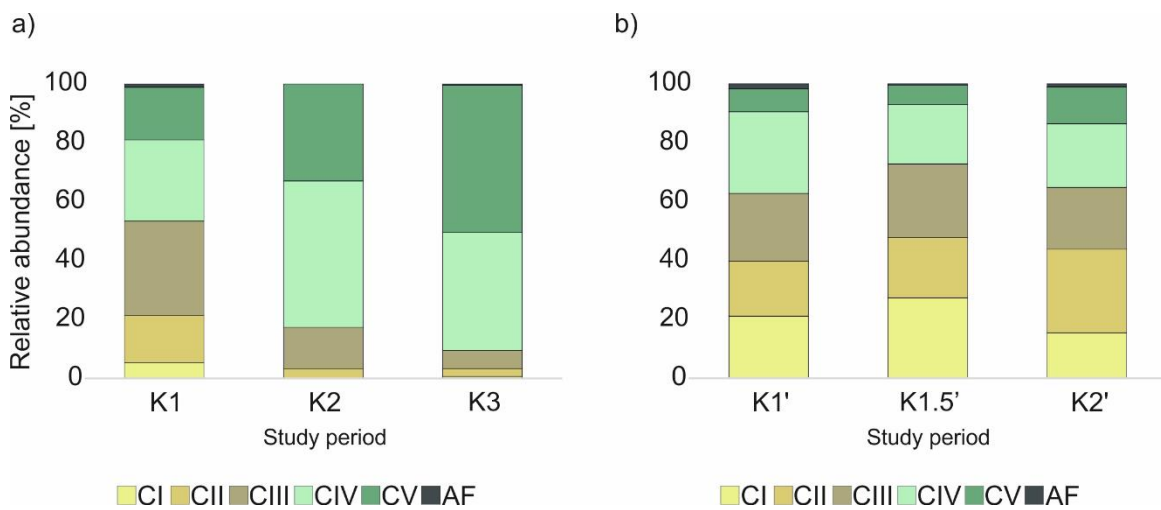


Fig. 16. *Calanus* spp. copepodite structure in Kongsfjorden in 2015 (a) and 2016 (b).

### Abundance

Generally CI and CII were more abundant in 2016 with the exception of higher abundance of CII in K1 than K1' (Table 11). Similarly to Hornsund, CIV was the most abundant stage in Kongsfjorden and reached very high abundance in 2015. The highest abundance of AF was observed in 2015.

## *Biomass*

In both years relatively low biomass were observed for the earliest copepodite stages CI and CII. Higher values for CIII was observed in 2015 (Table 11). High biomass of CIV was observed in 2015. The biomass of CV reached the highest values in comparison to the other stages in both study years with the maximum in 2015. Similarly to the earliest copepodite stages, the biomass of AF was relatively low throughout the study periods in both years.

Table 11. Abundance (ind. m<sup>-3</sup>) and biomass (g m<sup>-3</sup>) of *Calanus* spp. copepodite stages (CI-AF) from Kongsfjorden. *M* median, *Q*<sub>1</sub>-*Q*<sub>3</sub> percentiles 25-75%, *N* number of samples.

		<i>Calanus</i> spp. copepodite stage												<i>N</i>	
		CI		CII		CIII		CIV		CV		AF			
		<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>	<i>M</i>	<i>Q</i> <sub>1</sub> - <i>Q</i> <sub>3</sub>		
Study	Period	Year													
Abundance	K1	2015	121.3	48.0-228.0	364.0	204.0-430.0	642.0	414.0-812.0	558.0	396.7-723.3	275.3	190.0-432.0	18.7	12.0-32.0	9
	K2		0.0	0.0-22.0	22.0	0.0-533.3	1066.6	533.3-2880.0	10560.0	6932.6-11198.9	6932.6	6720.0-7999.2	0.0	0.0-89.0	5
	K3		8.33	0.0-13.3	18.7	13.3-42.7	46.0	28.0-106.7	297.2	197.3-864.0	439.7	119.1-896.0	6.8	1.8-7.1	6
	K1'	2016	160.0	136.0-180.0	122.2	100.0-136.0	184.0	132.0-200.0	232.0	126.7-240.0	48.0	28.0-120.0	12.0	8.0-15.6	9
	K1.5'		232.8	163.1-291.3	170.3	106.9-267.1	187.3	118.5-328.8	225.1	137.3-274.5	84.6	34.6-119.3	4.8	2.4-19.7	8
	K2'		213.3	128.0-360.0	320.0	296.0-613.3	293.3	168.0-464.0	416.0	160.0-544.0	144.0	85.3-240.0	17.8	4.0-24.9	9
Biomass	K1	2015	0.6	0.3-1.3	4.1	2.3-4.7	19.3	13.4-25.4	50.0	33.0-59.1	70.3	48.8-158.2	8.6	3.4-11.2	9
	K2		0.0	0.0-0.1	0.2	0.0-5.8	31.4	15.7-84.9	787.2	648.3-834.9	1697.4	1482.9-1711.1	0.0	0.0-25.1	5
	K3		0.0	0.0-0.1	0.2	0.1-0.5	1.3	0.8-3.1	24.0	15.4-75.0	101.0	26.2-217.6	3.0	0.5-5.6	6
	K1'	2016	0.9	0.8-1.1	1.4	1.2-1.5	5.4	3.9-6.3	22.3	11.9-26.2	23.2	13.8-66.3	6.7	4.2-7.5	9
	K1.5'		1.2	0.8-1.5	1.9	1.2-2.9	5.5	3.5-11.3	22.8	10.7-26.9	29.0	11.0-52.1	3.4	0.8-9.8	8
	K2'		1.1	0.7-1.8	3.5	3.2-6.7	8.6	5.0-13.7	33.60	13.8-43.5	48.6	18.2-64.2	5.6	3.5-7.5	9

## Hornsund vs. Kongsfjorden

*Calanus* spp. copepodite structure differed significantly between the two regions in comparable periods only in 2016 (Table 12). In 2015, the copepodite structure in both fjords was relatively similar (Fig. 17a) with the predominance of late stages (CIV and CV; Fig. 18a). In turn, in 2016 in the comparable H2' and K1.5' periods the copepodite structure differed significantly, which is demonstrated on the nMDS plot as a quite clear separation of these two groups of samples (Fig. 17b). In Kongsfjorden the high percentage of early stages CI-CIII was recorded. At the same time in Hornsund CIV prevailed (Fig. 18b).

Table 12. Results of two-factor multivariate PERMANOVA for the *Calanus* spp. copepodite structure in Hornsund and Kongsfjorden.

Year	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
2015	Fjord	1	642.8	3.35	0.054	8.35
2016	Fjord	1	5558.3	18.95	<b>0.001</b>	22.46

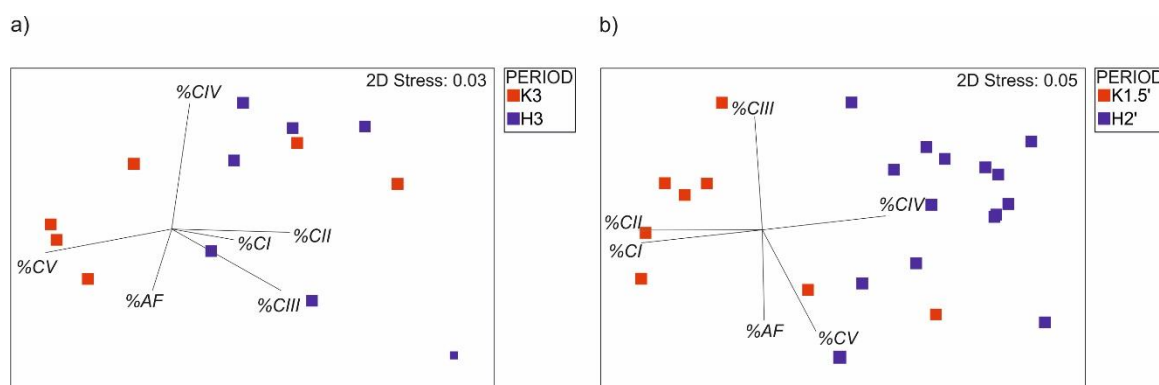


Fig. 17. The nMDS of the *Calanus* spp. copepodite structure in Kongsfjorden and Hornsund in 2015 (a) and 2016 (b). Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

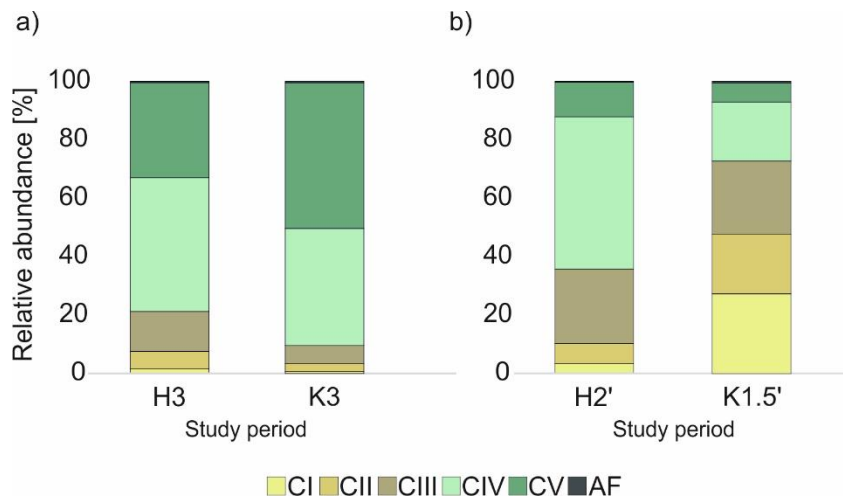


Fig. 18. Comparison of *Calanus* spp. copepodite structure in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b).

### 3.3.2 COPEPODITE STAGE INDEX

#### Hornsund

The *Calanus* spp. copepodite stage index differed between years and study periods (Table 13). Differences in the copepodite stage index had a stepwise character in both years, which is clearly illustrated on the box plots (Fig. 19a, b) with a slightly higher median values in all investigated periods observed in 2016.

Table 13. Results of two-factor multivariate PERMANOVA for the copepodite stage index for *Calanus* spp. in Hornsund.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Year	1	49.5	7.62	<b>0.014</b>	1.52
Period	2	746.9	57.56	<b>0.001</b>	5.07
Year x Period	2	24.1	1.86	0.154	0.89



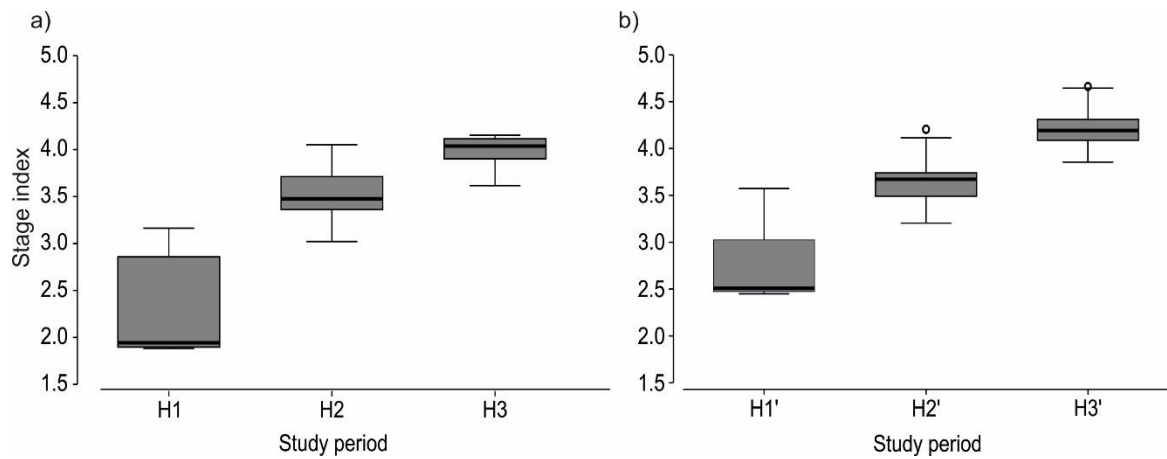


Fig. 19. Copepodite stage index for *Calanus* spp. in Hornsund in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

### Kongsfjorden

The *Calanus* spp. copepodite stage index differed between years but not between study periods (Table 14). The step wise character of the differences in copepodite stage index values between study periods were observed only in 2015 (Fig. 20a). In general, in 2015 median values of *Calanus* spp. copepodite stage index were higher than in 2016, when it remained relatively low (Fig. 20b).

Table 14. Results of two-factor multivariate PERMANOVA for the copepodite stage index for *Calanus* spp. in Kongsfjorden.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Year	1	698.1	46.40	<b>0.001</b>	5.59
Period	2	21.9	1.46	0.257	0.68
Year x Period	2	40.5	2.69	0.080	1.86

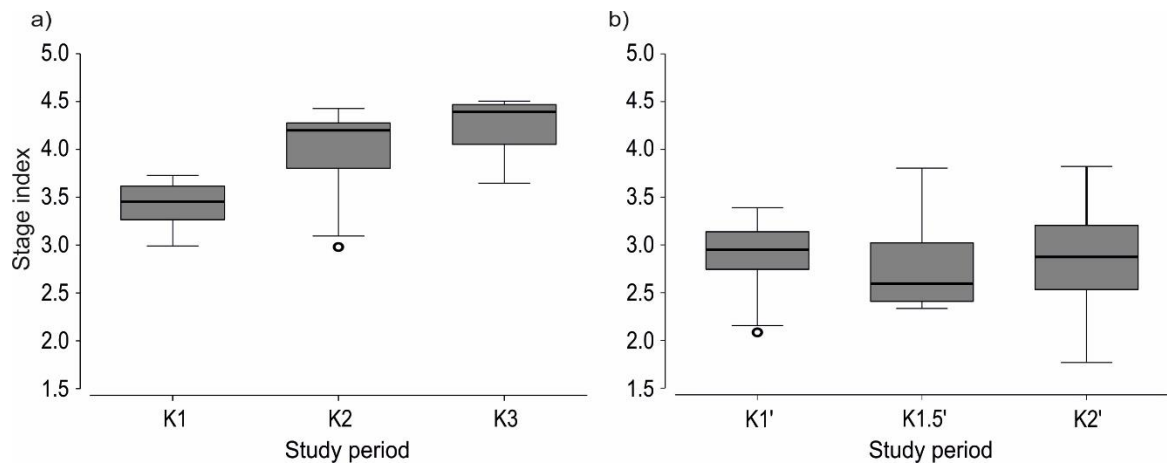


Fig. 20. Copepodite stage index for *Calanus* spp. in Kongsfjorden in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

### Hornsund vs. Kongsfjorden

The copepodite stage index for *Calanus* spp. differed between two fjords only in 2016 (Table 15), while in 2015 in corresponding study periods H3 and K3 it remained similar (Fig. 21a). In corresponding periods of 2016 (H2' and K1.5') higher median value was observed in Hornsund (Fig 21b).

Table 15. Results of two-factor multivariate PERMANOVA for the copepodite stage index for *Calanus* spp. in Kongsfjorden and Hornsund.

Year	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
2015	Fjord	1	7.9	2.91	0.116	0.89
2016	Fjord	1	258.5	34.61	<b>0.001</b>	4.90

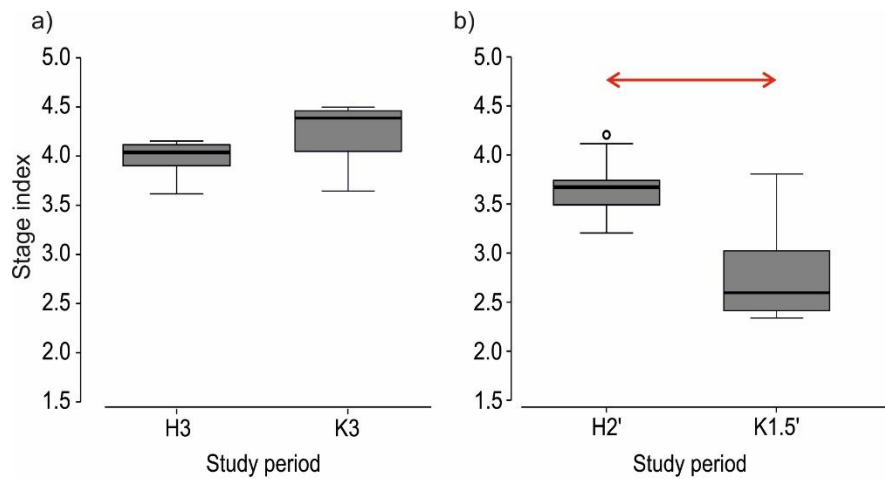


Fig. 21. Copepodite stage index for *Calanus* spp. in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b). Horizontal black lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range, red arrow shows statistically significant differences.

### 3.3.3 CALANUS SPP. POPULATION DEVELOPMENT MODEL

The assumptions of the simple population development model for two *Calanus* species, are described in details in the Materials and Methods chapter. The model was set to simulate the abundances and composition of copepodite and nauplii stages in three periods (corresponding to the periods of this study, i.e. from the beginning of July to the middle of August) under various temperature regimes occurring in Hornsund, separately for *C. glacialis* and *C. finmarchicus*. Initial abundance of individuals in each developmental stages in both species were determined on the basis of the average abundance of individuals from *in situ* data and are the same for two species in each scenario.

#### The stable scenario

##### *Calanus glacialis* in 3°C

The first scenario, assuming 3°C seawater temperature, low and optimal for the development of this species (Campbell et al. 2001; Daase et al. 2011; Grenvald et al. 2013), described the natural progress in *C. glacialis* development through the gradual aging of the population during summer (Fig. 22). In the second period, the model predicted the

occurrence of all copepodite stages with a distinct predominance of CIV, while in the third period only CIV and CV were predicted with a clear dominance of the latter one. The model did not predict the presence of nauplii in the second and third period since it was assumed that *C. glacialis* would no longer reproduce (see M&M for details).

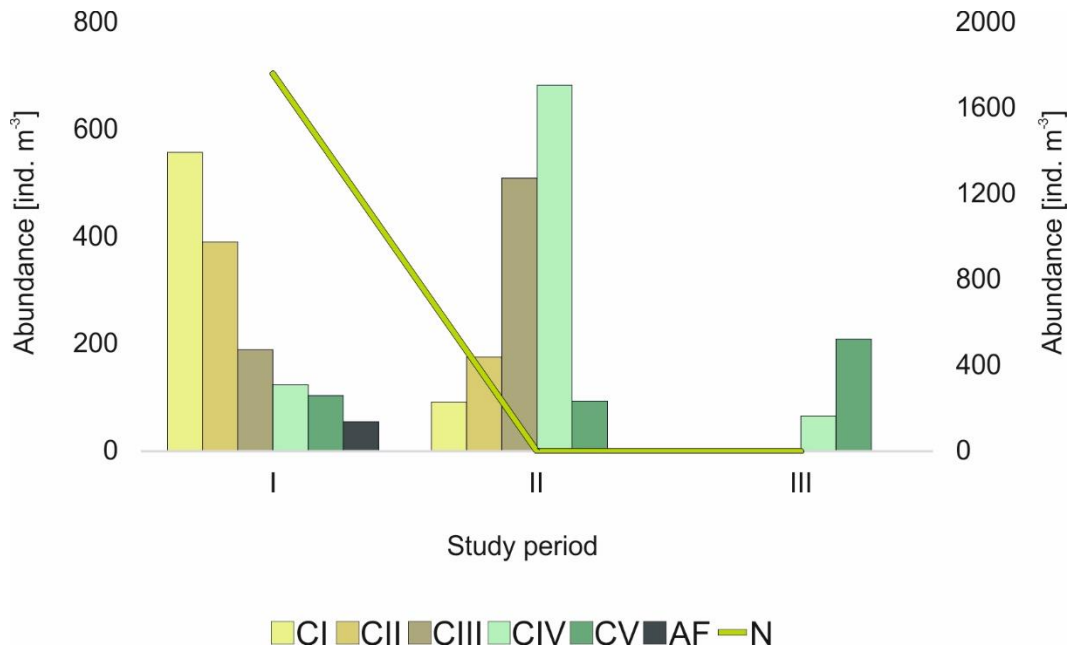


Fig. 22. Modelled abundance of *C. glacialis* copepodite stages (CI-AF) and nauplii (N, solid green line) under 3°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

### *Calanus finmarchicus* in 3°C

The scenario assuming the 3°C seawater temperature, low and less optimal for the development of this species (Campbell et al. 2001; Daase et al. 2011; Grenvald et al. 2013), described relatively natural progress in *C. finmarchicus* development through the gradual aging of the population but lasting only until the second period (Fig. 23). Then the model predicted the dominance of CIII and CIV. In the third period the younger population structure was predicted due to the higher abundances of early copepodite stages CI and CII.

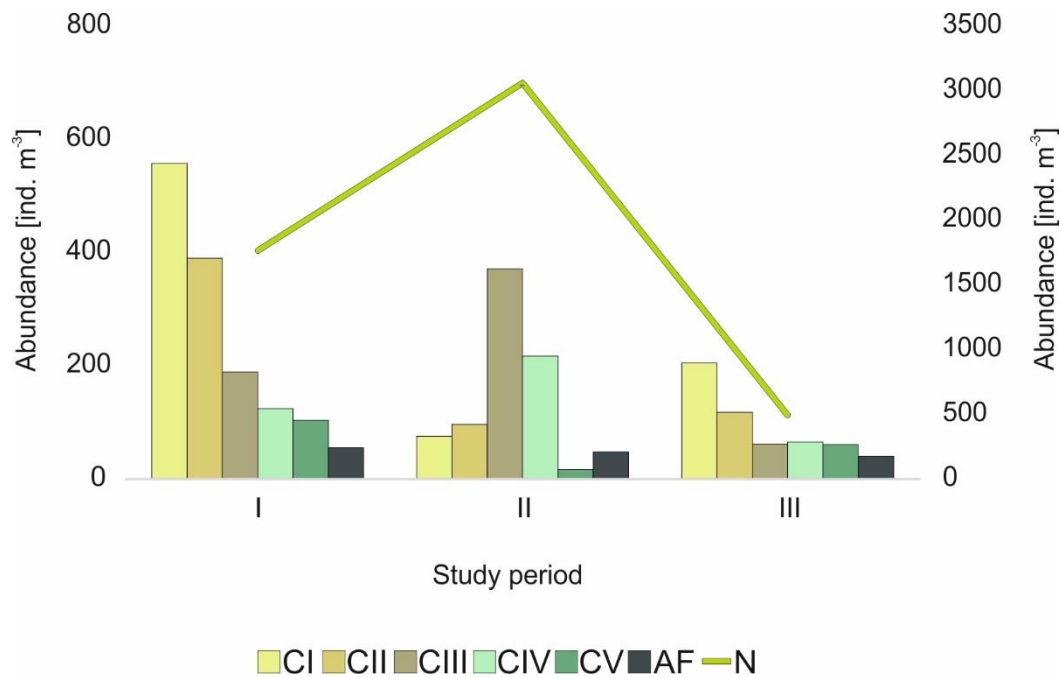


Fig. 23. Modelled abundance of *C. finmarchicus* copepodite stages (CI-AF) and nauplii (N, solid green line) under 3°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

### The warming scenario

#### *Calanus glacialis* in 6°C

The second scenario was assuming a seawater temperature rise to 6°C, which is considered to be the upper temperature limit for *C. glacialis* (Carstensen et al. 2012; Pasternak et al. 2013; Alcaraz et al. 2014). In this case differences in *C. glacialis* population development were not as gradual as in the previous model (Fig. 24). In the second period, the model predicted the presence exclusively of CIII-CV stages with a clear dominance of CIV accompanied by a high contribution of CV. In the third period only low abundance of CV was predicted. Similarly as in 3°C scenario the model did not predict the presence of nauplii in the second and third period.

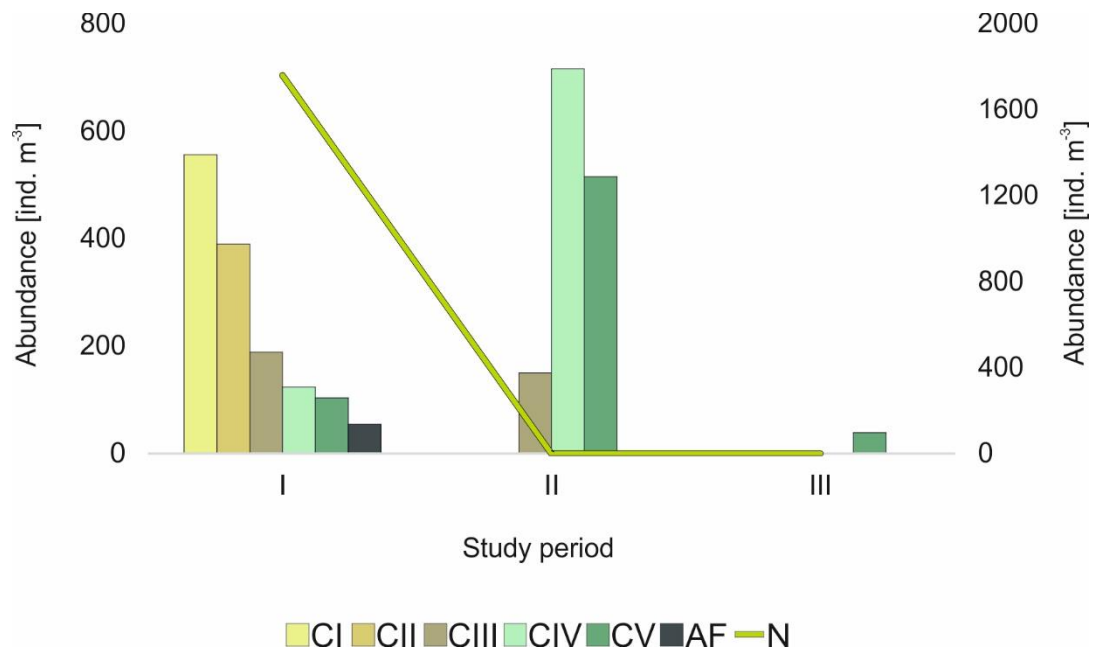


Fig. 24. Modelled abundance of *C. glacialis* copepodite stages (CI-AF) and nauplii (N, solid green line) under 6°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

### *Calanus finmarchicus* in 6°C

The second scenario assuming a seawater temperature rise to 6°C did not describe gradual progress in *C. finmarchicus* development since in all periods a relatively young population was predicted (Fig. 25). While in the second period the model predicted the dominance of CI and CIV, in the third period very high abundances of early copepodite stages CI-CIII and CIV were also expected.

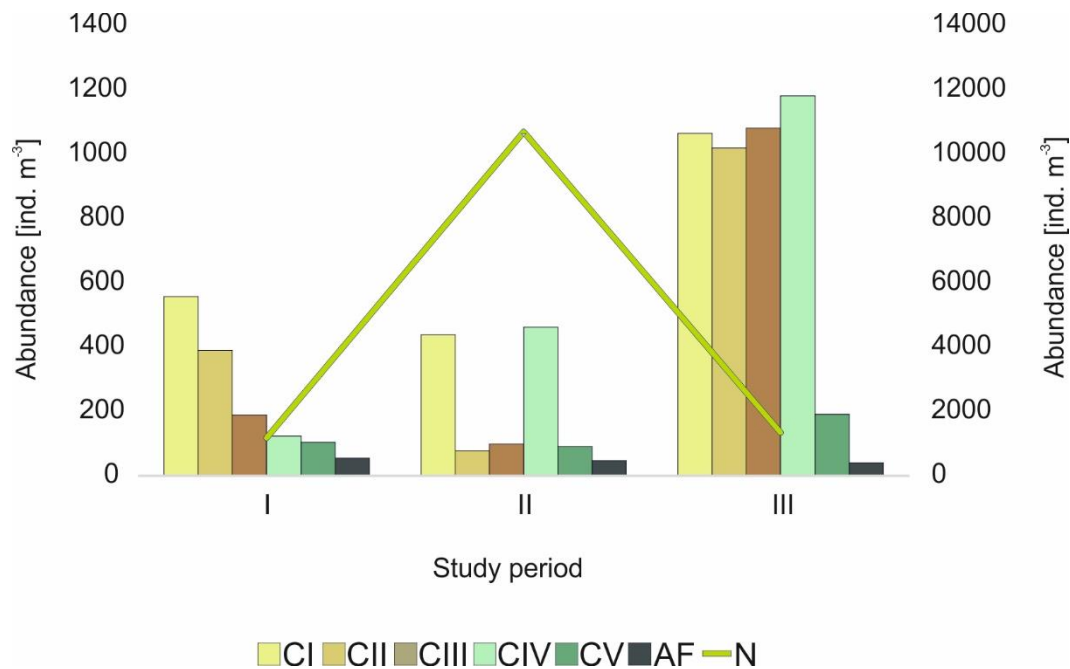


Fig. 25. Modelled abundance of *C. finmarchicus* copepodite stages (CI-AF) and nauplii (N, solid green line) under 6°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

### 3.4. CALANUS SPP. ON LITTLE AUKS' FORAGING GROUNDS

#### 3.4.1 CALANUS SPP. FIFTH COPEPODITE STAGE ON FORAGING GROUNDS

##### Hornsund

The percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Hornsund did not differ between years but there were differences between some of the study periods (Table 16). In both years differences in percentage of CV biomass in total zooplankton biomass had a moderate, step wise character, marked more clearly in 2015, and increased from 20-30% up to approximately 60% at the end of the study periods (Fig. 26a, b).

Table 16. Results of two-factor multivariate PERMANOVA for the percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Hornsund.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Year	1	23.3	0.05	0.985	-5.00	
Period	2	4166.6	8.48	<b>0.001</b>	16.05	1,3; 2,3
Year x Period	2	204.4	0.42	0.803	-6.34	

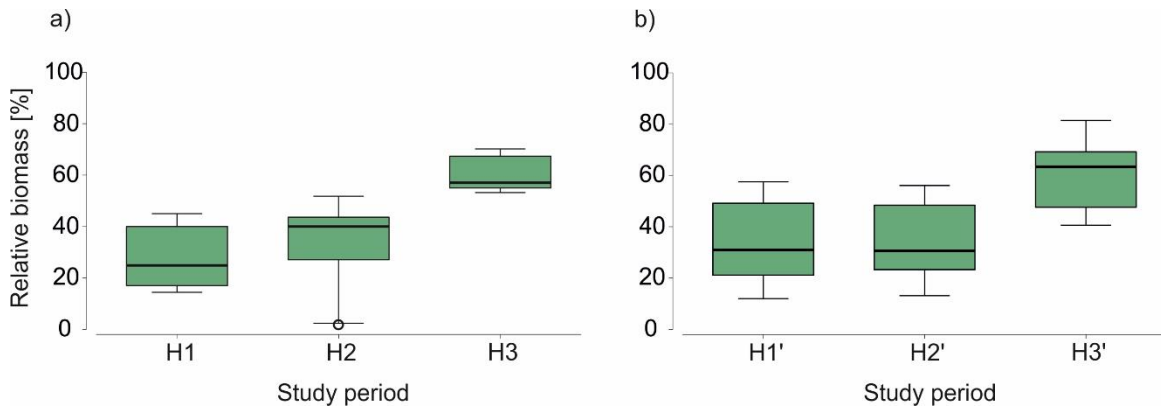


Fig. 26. Percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Hornsund in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

### Kongsfjorden

In Kongsfjorden a different pattern was observed. Differences were found only between the years (Table 17). In 2015 the percentage of CV biomass in total zooplankton biomass was relatively high and increased slightly from ~50% to ~70% in the last study period, while in 2016 they remained relatively low (~20%) and stable throughout the entire study season (Fig. 27a, b).



Table 17. Results of two-factor multivariate PERMANOVA for the percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Kongsfjorden.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Year	1	15943.0	21.26	<b>0.001</b>	26.39
Period	2	493.2	0.66	0.661	-4.18
Year x Period	2	1234.8	1.65	0.145	8.12

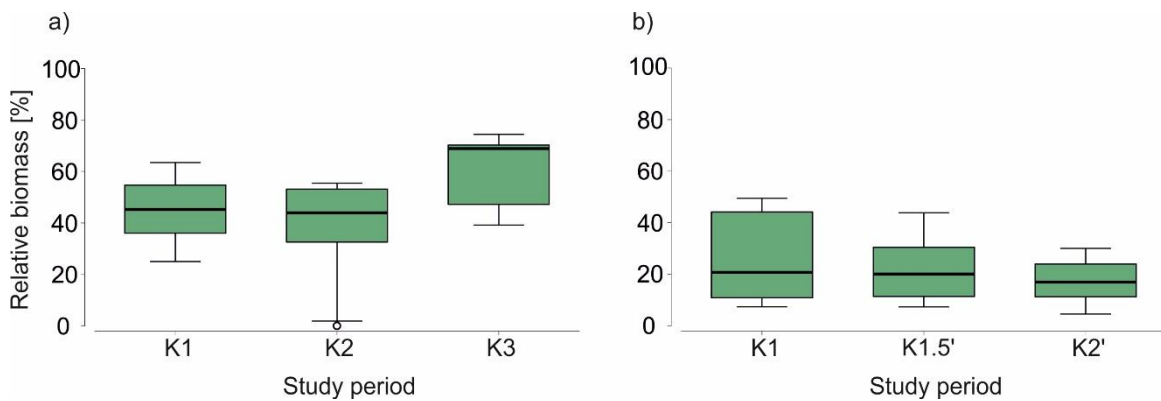


Fig. 27. Percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Kongsfjorden in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

### Hornsund vs. Kongsfjorden

The percentage of *Calanus* spp. CV biomass of in total zooplankton biomass did not differ between two studied fjords, in both years (Table 18). The median values in comparable periods were similar and differed by only about 10%. In 2015 slightly higher values were indicated in Kongsfjorden, while in 2016 in Hornsund (Fig. 28).

Table 18. Results of two-factor multivariate PERMANOVA for the percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Hornsund and Kongsfjorden.

Year	Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
2015	Fjord	1	0.6	0.03	0.873	-1.90
2016	Fjord	1	616.6	3.62	0.061	6.54

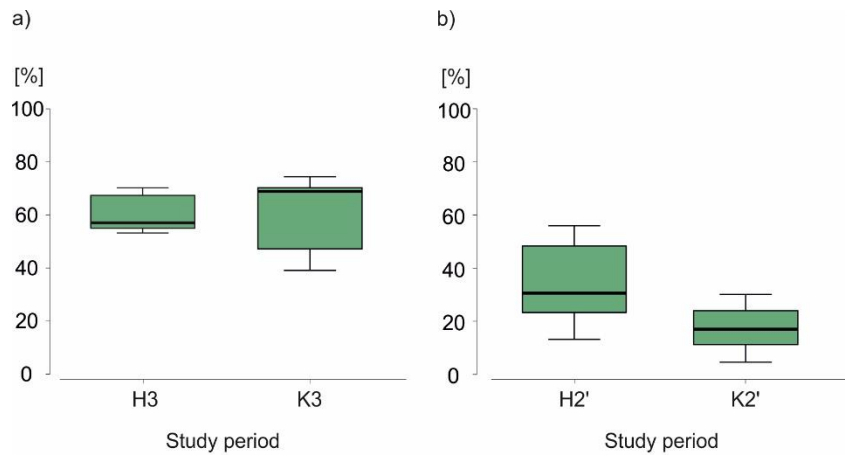


Fig. 28. Percentage of *Calanus* spp. CV biomass in total zooplankton biomass in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represents quartiles, whiskers ranges, dots are values outside the range.

### 3.4.2. SPATIAL DISTRIBUTION OF *CALANUS* SPP. IN RELATION TO ENVIRONMENTAL VARIABLES

#### Hornsund

The LOPC-CTD-F data collected at the end of July in 2015 indicated that patches with the highest percentage of *Calanus* spp. fraction (1 – 2.5mm) were concentrated either in cold (4-5°C), less saline (33-34) Arctic-type waters, or in the transition zone between Arctic and Atlantic waters (Fig. 29). The DistLM procedure confirmed a significant effects of seawater temperature, salinity and chlorophyll fluorescence on the percentage of *Calanus* spp. fraction in overall mesozooplankton abundance recorded by LOPC (Table 19). All the above mentioned environmental variables explained 20% of total variability observed in the *Calanus* spp. fraction percentage. The strongest influence on the observed variations was caused by salinity (10%, Table 19, Fig. 30).

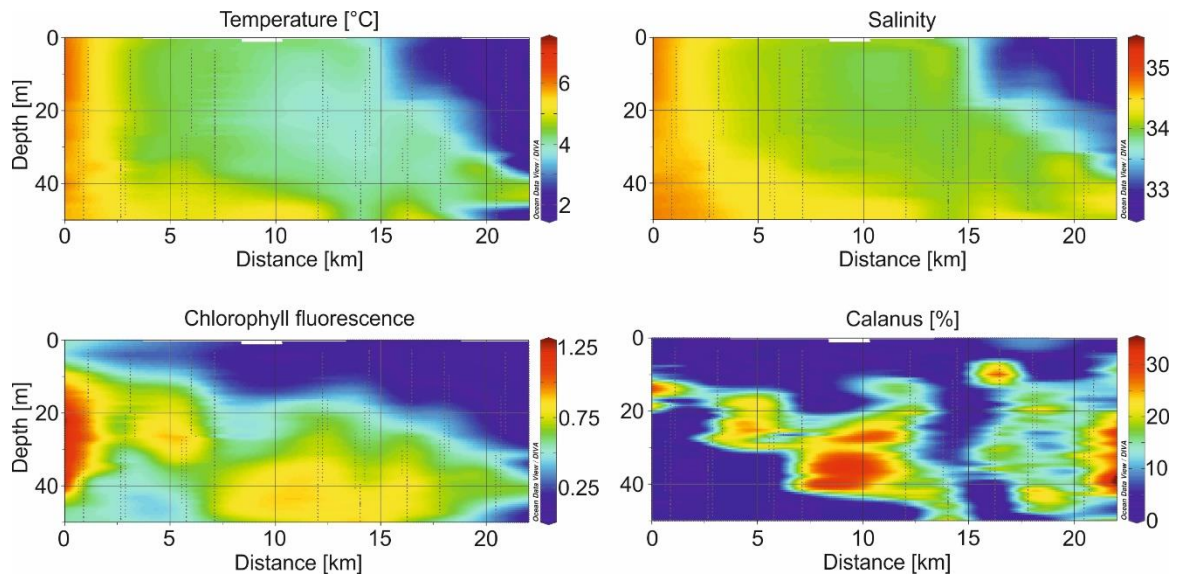


Fig. 29. Spatial distribution of environmental variables and percentage of *Calanus* spp. fraction in mesozooplankton community along Hornsund cross-section in 2015.

Table 19. Results of the DistLM analysis for fitting environmental variables to the percentage of *Calanus* spp. fraction. Var% - percentage of explained variance; Cum% - cumulative percentage explained by the added variable.

Marginal tests				Sequential tests					
Variable	Pseudo-F	<i>p</i>	Var%	Variable	R <sup>2</sup>	Pseudo-F	<i>p</i>	Var%	Cum%
<b>Hornsund 2015</b>									
Salinity	81.62	<b>0.001</b>	0.04	Salinity	0.04	81.62	<b>0.001</b>	0.04	0.4
Chlorophyll fluorescence	47.87	<b>0.001</b>	0.02	+Chlorophyll fluorescence	0.18	307.13	<b>0.001</b>	0.14	0.18
Temperature	16.97	<b>0.001</b>	<0.01	+Temperature	0.20	48.00	<b>0.001</b>	0.02	0.20
<b>Hornsund 2016</b>									
Salinity	748.66	<b>0.001</b>	0.19	Salinity	0.19	748.66	<b>0.001</b>	0.19	0.19
Chlorophyll fluorescence	1.44	0.226	<0.01	+Chlorophyll fluorescence	0.22	113.97	<b>0.001</b>	0.03	0.22
Temperature	26.96	<b>0.001</b>	0.01	+Temperature	0.23	51.16	<b>0.001</b>	0.01	0.23
<b>Kongsfjorden 2015</b>									
Temperature	1003.50	<b>0.001</b>	0.19	Temperature	0.19	1003.50	<b>0.001</b>	0.19	0.19
Chlorophyll fluorescence	410.79	<b>0.001</b>	0.09	+Chlorophyll fluorescence	0.29	585.56	<b>0.001</b>	0.10	0.29
Salinity	121.26	<b>0.001</b>	0.03	+Salinity	0.29	13.64	<b>0.001</b>	<0.01	0.29
<b>Kongsfjorden 2016</b>									
Temperature	924.14	<b>0.001</b>	0.20	Temperature	0.20	924.14	<b>0.001</b>	0.20	0.20
Chlorophyll fluorescence	104.66	<b>0.001</b>	0.03	+Chlorophyll fluorescence	0.20	29.51	<b>0.001</b>	<0.01	0.20
Salinity	172.59	<b>0.001</b>	0.04	+Salinity	0.22	87.95	<b>0.001</b>	0.02	0.22

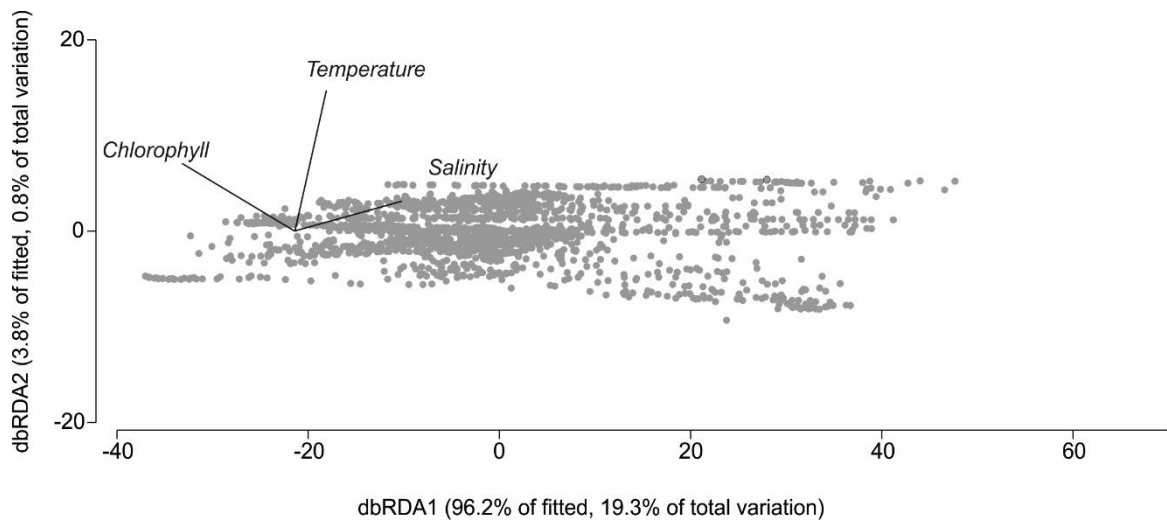


Fig. 30. Distance-based redundancy plot (dbRDA) illustrating the relationship of the *Calanus* spp. percentage in relation to environmental variables in Hornsund in 2015. Vectors indicate the direction of best correlating variables.

In 2016, patches with the highest percentage of *Calanus* spp. fraction were concentrated mainly in cold (4-5°C), low-saline (~34) upper 20 m water layer, with elevated chlorophyll fluorescence values (Fig. 31). Similarly to 2015, environmental variables explained 23% of the overall variability in percentage of *Calanus* spp. fraction. Salinity had the greatest impact (19%) however no effect of chlorophyll fluorescence was observed (Table 19, Fig. 32).

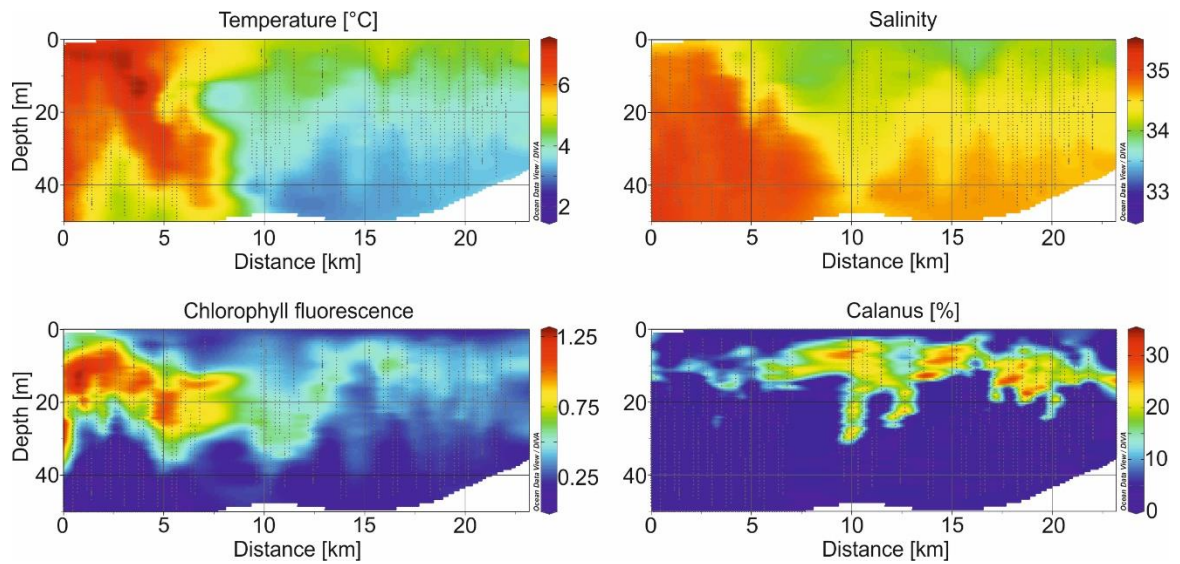


Fig. 31. Spatial distribution of environmental variables and percentage of *Calanus* spp. fraction in mesozooplankton community along Hornsund cross-section in 2016.

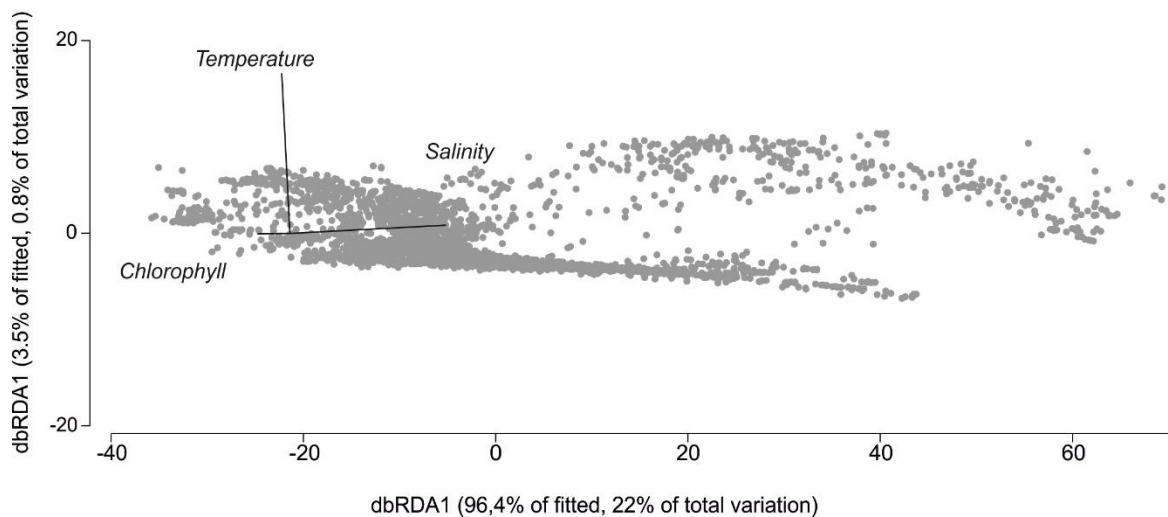


Fig. 32. Distance-based redundancy plot (dbRDA) illustrating the relationship of the *Calanus* spp. percentage in relation to environmental variables in Hornsund in 2016. Vectors indicate the direction of best correlating variables.

### Kongsfjorden

In 2015 patches with the higher percentage of *Calanus* spp. fraction were concentrated mainly in relatively warm ( $>6^{\circ}\text{C}$ ), less saline (32-33) upper 20 m water layer (Fig. 33). The DistLM procedure confirmed a significant effects of seawater temperature, salinity and chlorophyll fluorescence on the percentage of *Calanus* spp. fraction in overall



mesozooplankton abundance recorded by LOPC (Table 19). All the above mentioned environmental variables explained 29% of total variability observed in the *Calanus* spp. percentage. The greatest effect on the observed variations was caused by temperature (19%, Table 19, Fig. 34).

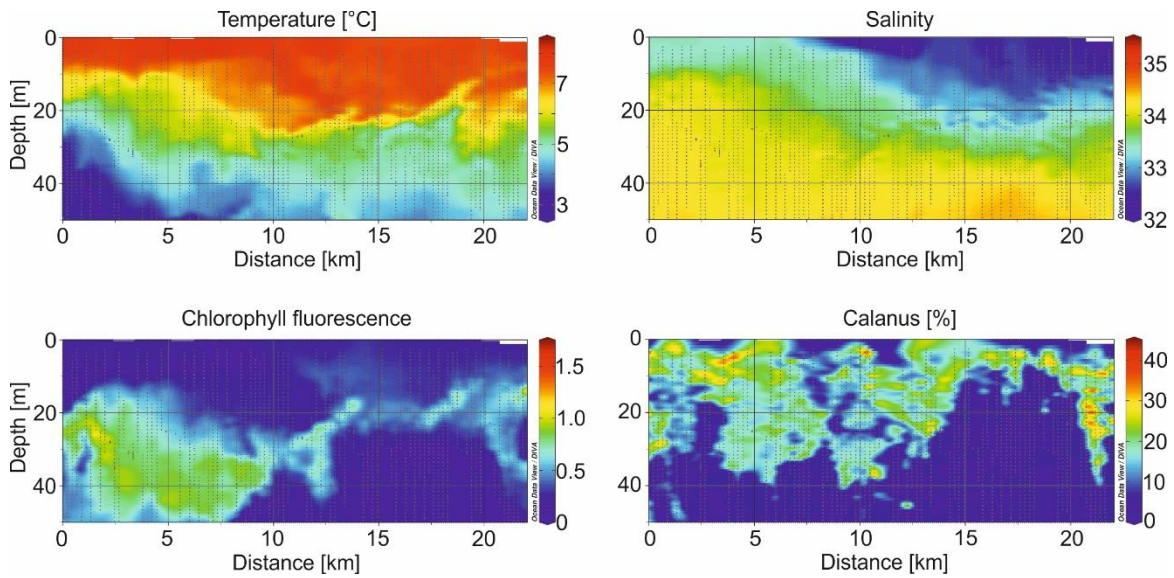


Fig. 33. Spatial distribution of environmental variables and percentage of *Calanus* spp. fraction in mesozooplankton community along Kongsfjorden cross-section in 2015.

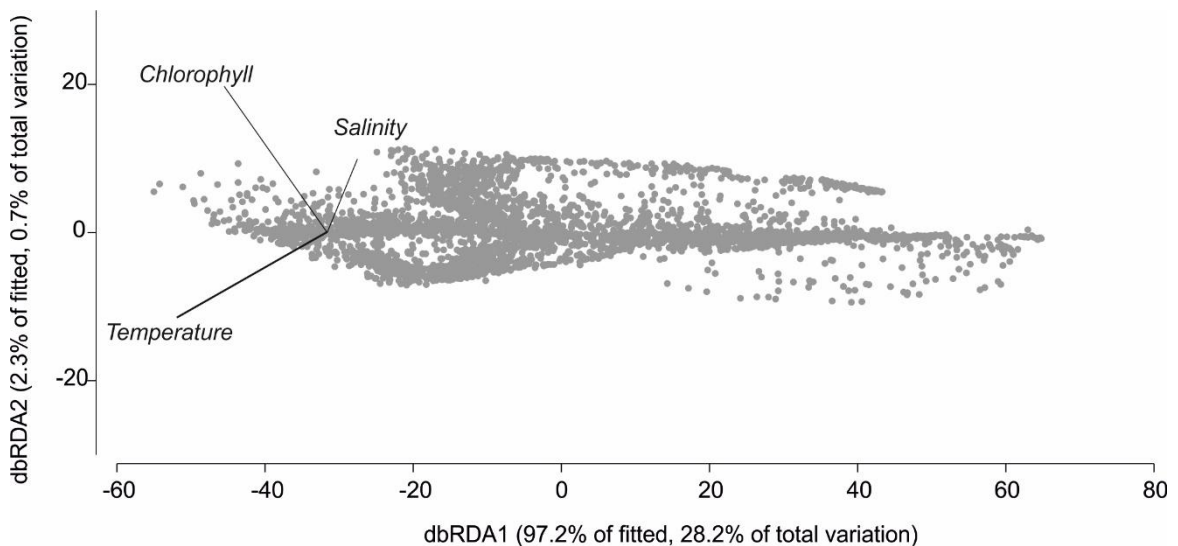


Fig. 34. Distance-based redundancy plot (dbRDA) illustrating the relationship of the *Calanus* spp. percentage in relation to environmental variables in Kongsfjorden in 2015. Vectors indicate the direction of best correlating variables.

In 2016, the patches with higher percentage of *Calanus* spp. in mesozooplankton community were also concentrated mainly in relatively warm ( $>6^{\circ}\text{C}$ ), less saline (33-34) upper 20 m water layer, just above the layer with higher chlorophyll fluorescence (Fig. 35). Environmental variables explained 22% of the total variability of the *Calanus* spp. fraction percentage with almost entire variability explained by temperature (20%, Table 19, Fig. 36).

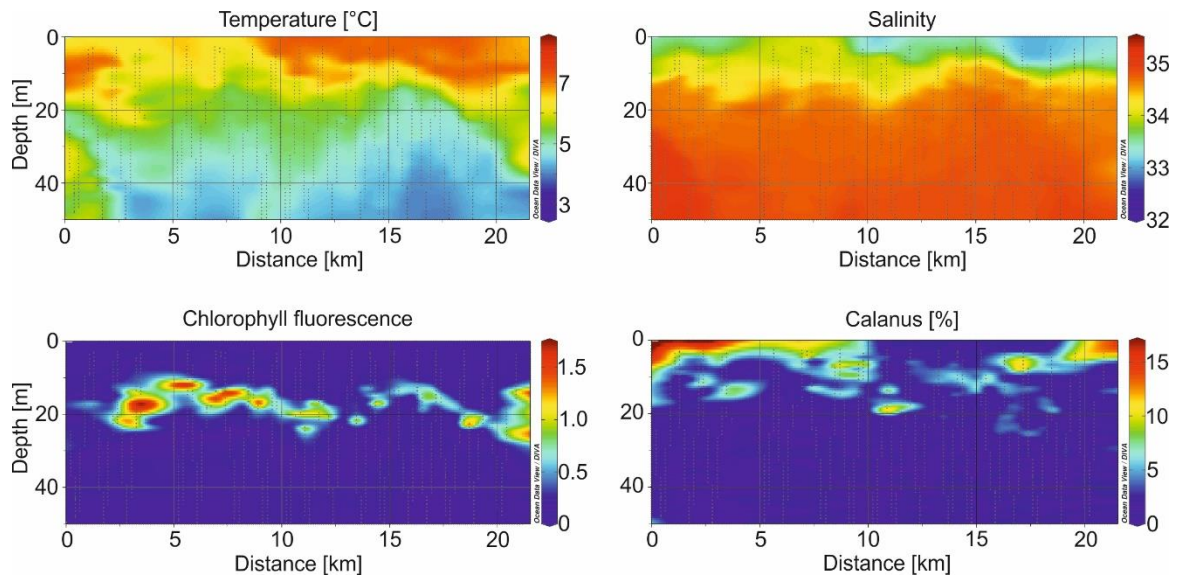


Fig. 35. Spatial distribution of environmental variables and percentage of *Calanus* spp. fraction in mesozooplankton community along Kongsfjorden cross-section in 2016.



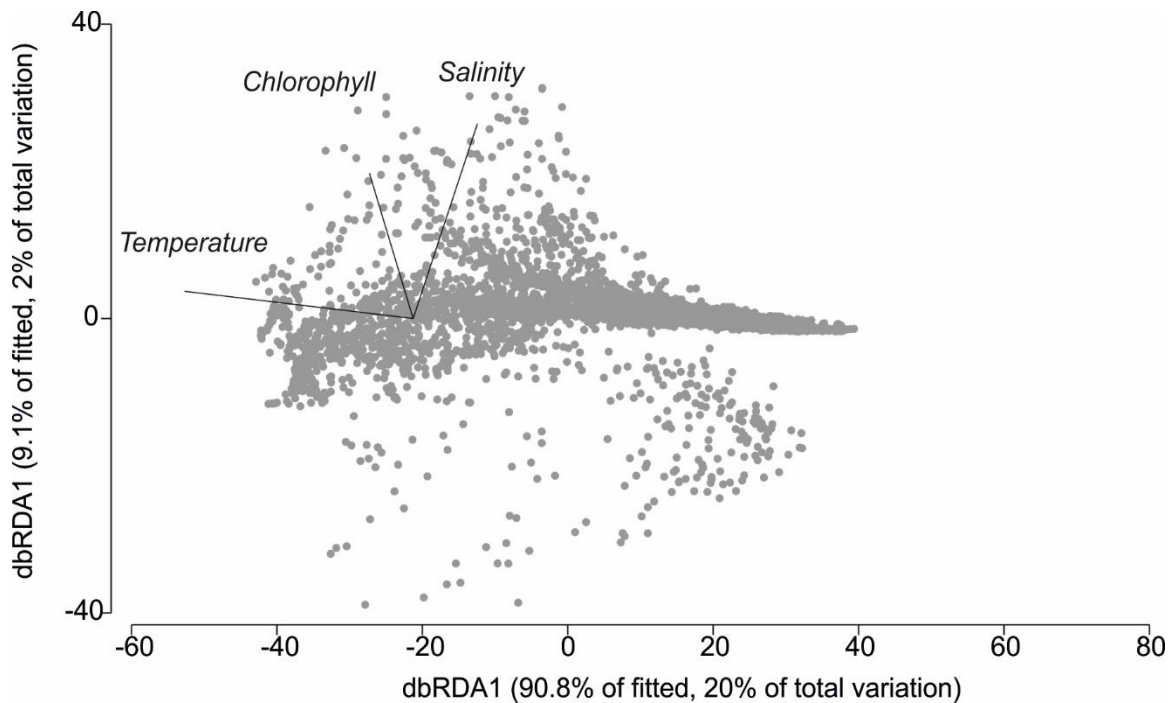


Fig. 36. Distance-based redundancy plot (dbRDA) illustrating the relationship of the *Calanus* spp. percentage in relation to environmental variables in Kongsfjorden in 2016. Vectors indicate the direction of best correlating variables.

### 3.4.3. CALANUS SPP. IN LITTLE AUKS DIET

#### Hornsund colony

Diet composition of little auk chicks in Hornsund colony in 2015 differed significantly between all three periods corresponding to specific chicks' weeks of life (Table 20). A clear separation of the three investigated periods was shown on the nMDS plot (Fig. 37). Samples from Hc2 and Hc3 were grouped more closely together, since one taxa - *Apherusa glacialis* constituted more than 90% of total biomass in vast majority of samples from these periods (Fig. 38). In turn, in most of the samples from Hc1 *Calanus* spp. CV dominated. However in several samples from this period 80% of zooplankton biomass was represented by *Thysanoessa inermis*. Another important food items for the little auk chicks in Hc1 were *Calanus* spp. AF and *Eupagurus* zoea. SIMPER analyses confirmed that the average dissimilarity between the diet composition of the Hc1 vs. Hc2 (89%), and the Hc1 vs. Hc3 (86%) was high (Table 21). Species responsible the most for this dissimilarity were *Apherusa glacialis*, *Calanus* spp. CV and *T. inermis*.

Table 20. Results of one-factor multivariate PERMANOVA for the little auk chicks' diet composition in Hornsund and Kongsfjorden colony with study period as a factor.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Period	2	47250.0	68.94	<b>0.001</b>	50.19	Hc1≠Hc2; Hc1≠Hc3; Hc2≠Hc3

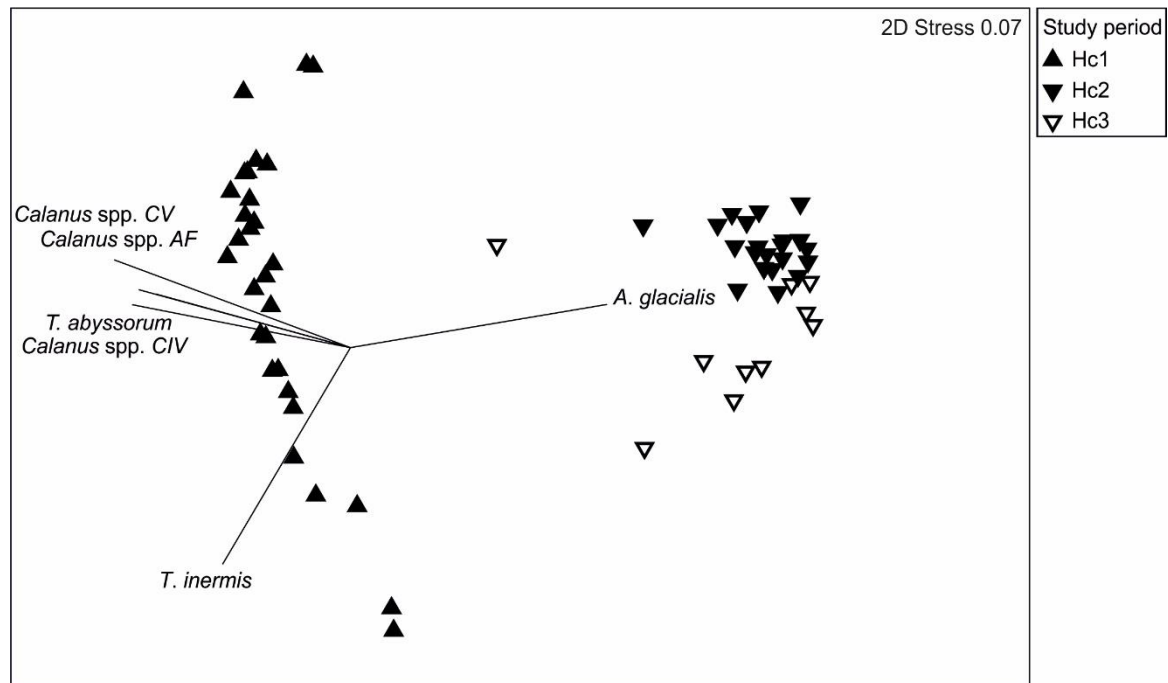


Fig. 37. The nMDS of the little auk chicks' diet composition in Hornsund colony in 2015. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

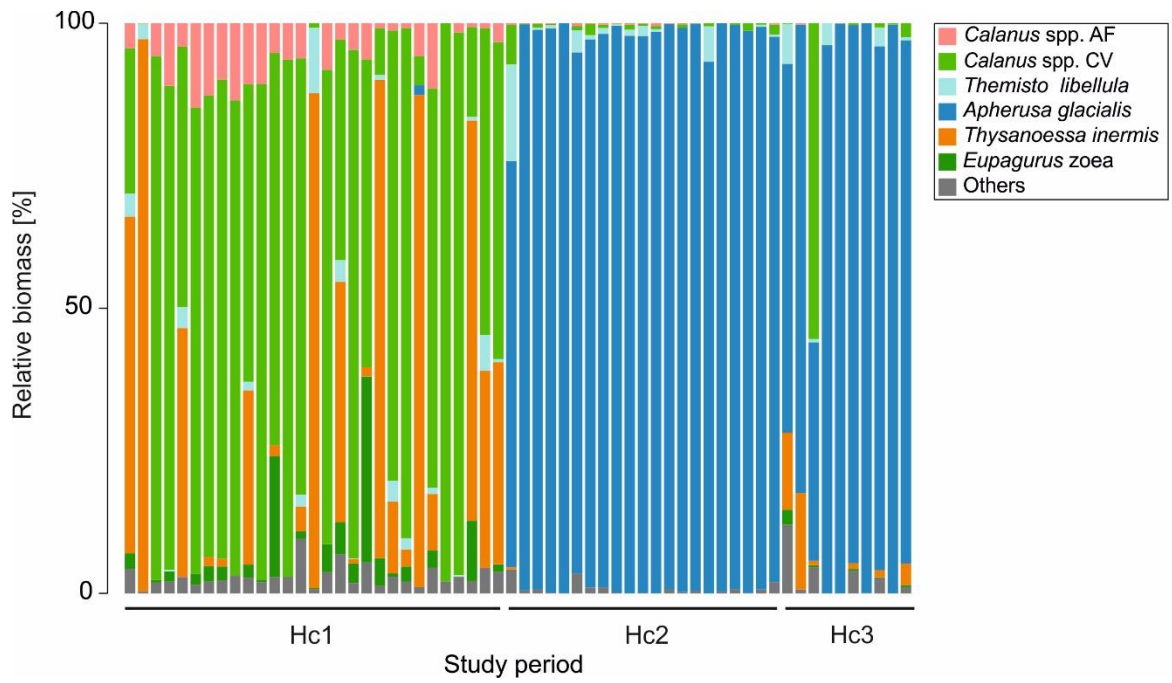


Fig. 38. Little auk chicks' diet composition in samples collected in Hornsund colony in 2015.

Table 21. SIMPER analysis for the taxa contributing > 5% for dissimilarities between the study periods in Hornsund colony in 2015 and 2016.

	Average abundance		Average diss.	Diss/SD	Contribution (%)	Cumulative (%)
<b>Hc1 vs. Hc2</b>						
Average dissimilarity = 88.92%	Hc1	Hc2				
<i>Apherusa glacialis</i>	0.14	33.54	35.30	4.83	39.70	39.70
<i>Calanus</i> spp. CV	21.59	2.50	20.04	1.98	22.54	62.24
<i>Thysanoessa inermis</i>	10.04	0.11	10.20	0.95	11.47	73.71
<b>Hc1 vs. Hc3</b>						
Average dissimilarity = 85.53%	Hc1	Hc3				
<i>Apherusa glacialis</i>	0.14	21.80	25.91	3.25	30.29	30.29
<i>Calanus</i> spp. CV	21.59	2.82	22.56	1.89	26.37	56.67
<i>Thysanoessa inermis</i>	10.04	2.93	10.87	1.02	12.71	69.38
<i>Calanus</i> spp. AF	5.88	0.17	6.62	1.83	7.74	77.11
<b>Hc2 vs. Hc3</b>						
Average dissimilarity = 36.59%	Hc2	Hc3				
<i>Apherusa glacialis</i>	33.54	21.80	14.80	2.29	40.46	40.46
<i>Calanus</i> spp. CV	2.50	2.82	4.01	0.78	10.97	51.42
<i>Themisto libellula</i>	2.81	1.91	3.66	1.08	10.01	61.43
<i>Thysanoessa inermis</i>	0.11	2.93	3.52	0.85	9.62	71.04
<b>Hc2' vs. Hc3'</b>						
Average dissimilarity = 26.58%	Hc2'	Hc3'				
<i>Calanus</i> spp. CV	27.21	31.60	6.78	1.43	25.52	25.52
<i>Calanus</i> spp. AF	8.66	8.73	3.73	1.20	14.03	39.54
<i>Eupagurus zoea</i>	2.54	3.93	3.57	1.15	13.44	52.98
<i>Themisto libellula</i>	1.92	0.67	2.06	0.63	7.75	60.73
<i>Hyas zoea</i>	1.24	1.56	1.75	0.94	6.59	67.32
<i>Calanus</i> spp. CIV	2.75	3.04	1.51	1.37	5.69	73.02

Little auk chicks' diet composition in Hornsund colony in 2016 also differed among study periods significantly (Table 22). A separation was however not so clear and samples on the nMDS plot were clustered closely together (Fig. 39), since in both study periods in all diet samples *Calanus* spp. CV dominated the total zooplankton biomass (Fig. 40). An important component of the diet in Hc2' and Hc3' was also *Calanus* spp. AF. SIMPER analysis indicated that the average dissimilarity between the diet composition in these periods was relatively low, and was influenced mostly by *Calanus* spp. CV, *Calanus* spp. AF and *Eupagurus zoea* (Table 21).

Table 22. Results of two-factor multivariate PERMANOVA for the little auk chicks' diet composition in Hornsund 2016.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Period	1	991.4	2.81	<b>0.011</b>	5.58

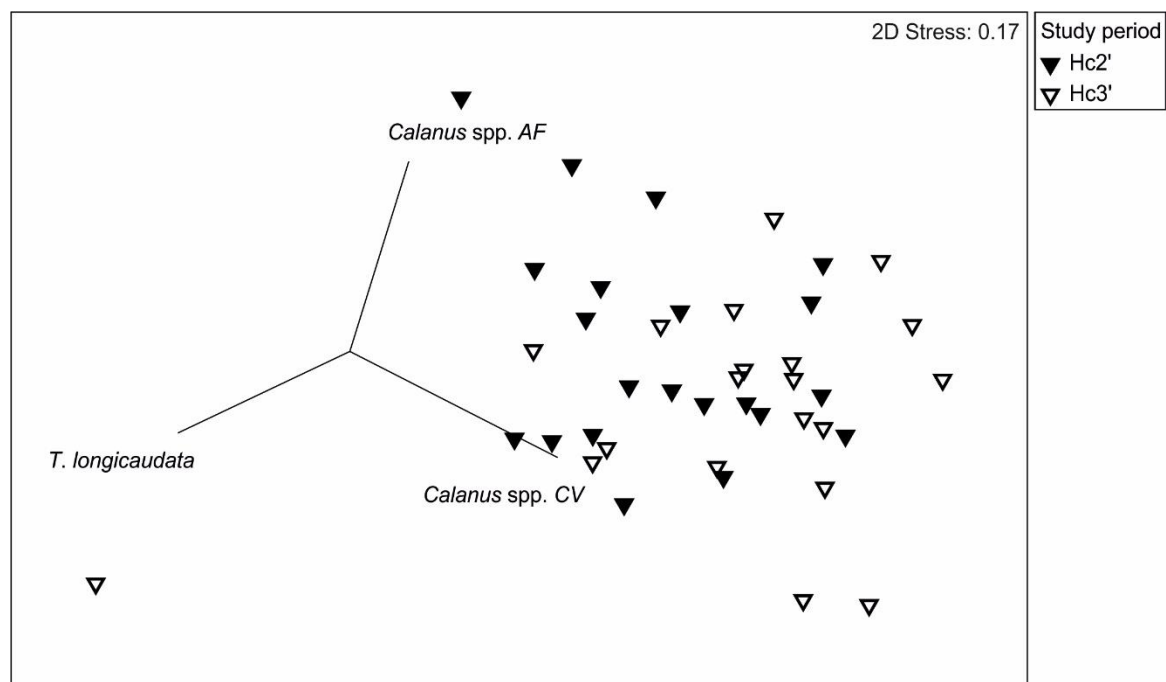


Fig. 39. The nMDS of the little auk chicks' diet composition in Hornsund colony in 2016. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

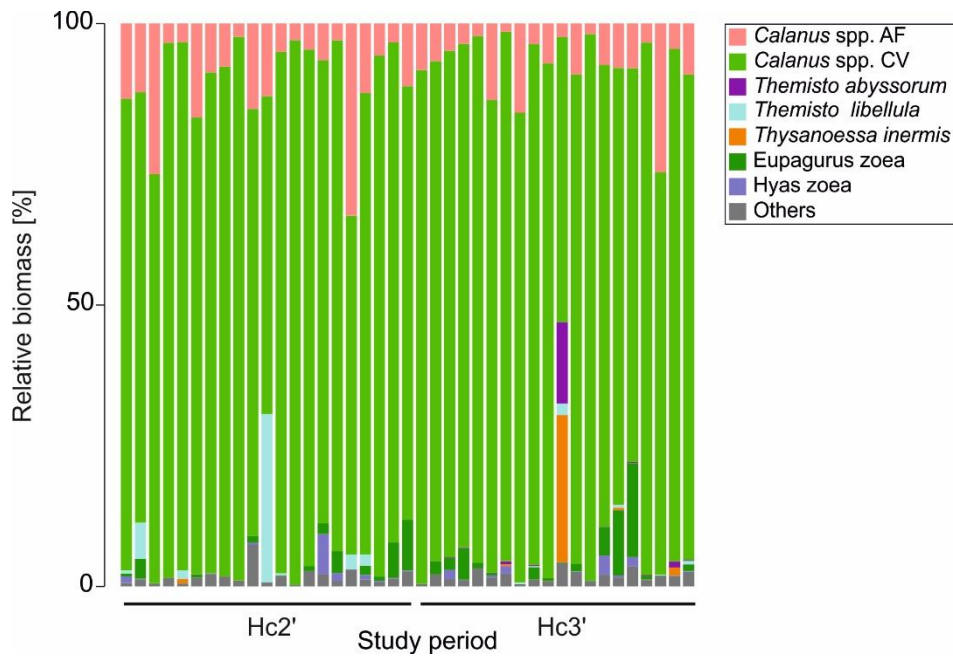


Fig. 40. Little auk chicks' diet composition in samples collected in Hornsund colony in 2016.

### Kongsfjorden colony

Little auk chicks' diet composition in Kongsfjorden colony in 2015 did not differ among study periods significantly (Table 23). In both study periods in most samples *Calanus* spp. CV dominated the total zooplankton biomass with the exception of two samples consisting almost completely of *C. hyperboreus* and *T. inermis* (Fig. 41). An important component of the diet were also *T. abyssorum* and *Calanus* spp. AF.

Table 23. Results of two-factor multivariate PERMANOVA for the little auk chicks' diet composition in Kongsfjorden colony in 2015.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Period	1	1065.3	0.75	0.607	-7.19

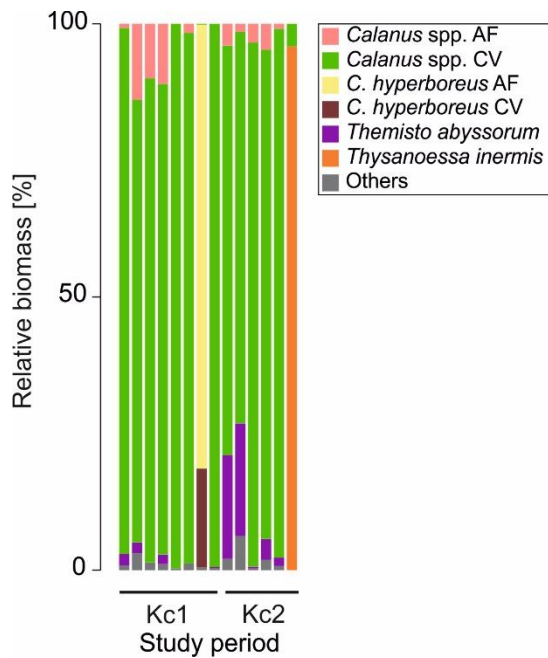


Fig. 41. Little auk chicks' diet composition in samples collected in Kongsfjorden colony in 2015.

In 2016, similarly, in 2016 *Calanus* spp. CV dominated the total zooplankton biomass in most of the diet samples. Only two samples were consisting almost completely *T. inermis* (Fig. 42). An important components of the diet were also *T. libellula* and *Calanus* spp. AF.

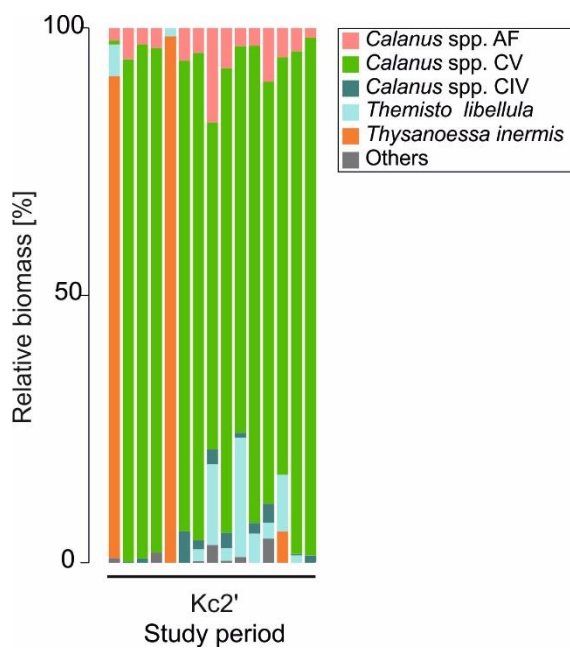


Fig. 42. Little auk chicks' diet composition in samples collected in Kongsfjorden colony in 2016.

## Kongsfjorden colony vs. Hornsund colony

Little auk chicks' diet composition in samples collected in comparable periods in Hornsund and Kongsfjorden colonies in 2015 (Hc1 and Kc1) differed significantly (Table 24). A separation was however not clear and samples on the nMDS plot were grouped relatively closely together (Fig. 43), since in both study periods in most diet samples *Calanus* spp. CV dominated the total zooplankton biomass. SIMPER analysis indicated that the average dissimilarity between the diet composition in both study periods in two colonies was moderately high, and was influenced mostly by *Calanus* spp. CV, *T. inermis* (which was observed only in samples from Hc1) and *Calanus* spp. AF (Table 25). *Themisto libellula* was observed also in samples from Hc1, but contributed less to overall dissimilarity.

Table 24. Results of two-factor multivariate PERMANOVA for the little auk chicks' diet composition in Hornsund and Kongsfjorden in 2015.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Colony	1	6211.6	5.72	<b>0.003</b>	20.22

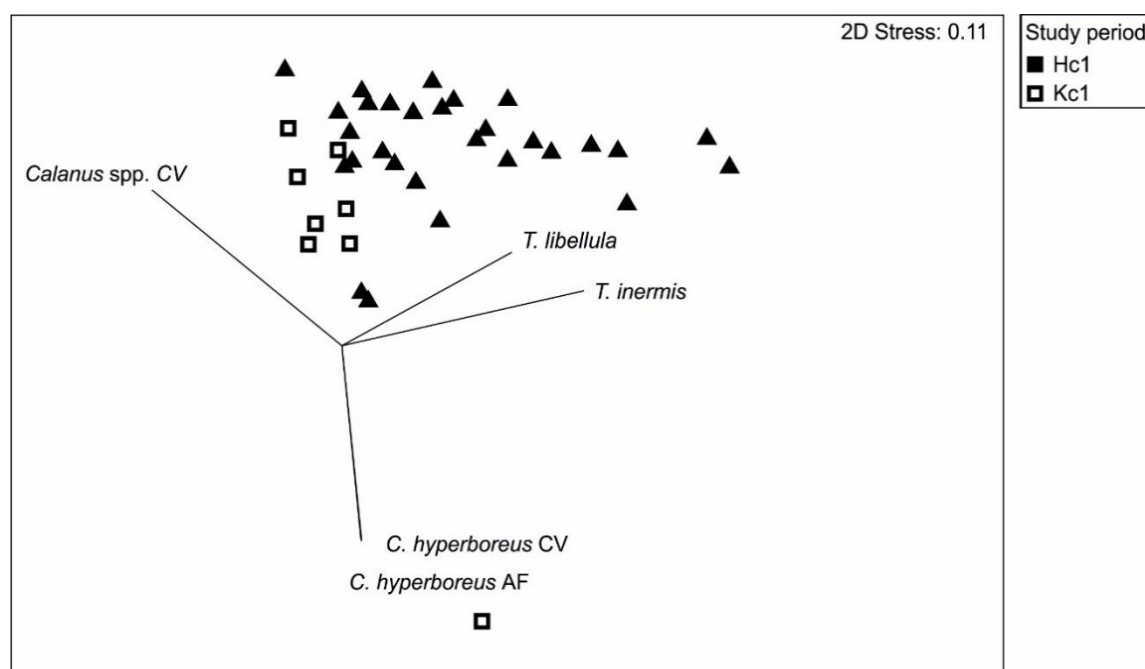


Fig. 43. The nMDS of the little auk chicks' diet composition in Hornsund and Kongsfjorden colony in 2015. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.



Table 25. SIMPER analysis for the taxa contributing > 5% for dissimilarities between the comparable study periods in Hornsund and Kongsfjorden colony in 2015 and 2016.

	Average abundance		Average diss.	Diss/SD	Contribution (%)	Cumulative (%)
<b>Hc1 vs. Kc1</b>						
Average dissimilarity = 52.27%	Hc1	Kc1				
<i>Calanus</i> spp. CV	21.59	20.20	12.60	1.21	24.10	24.10
<i>Thysanoessa inermis</i>	10.04	0.00	11.55	0.94	22.10	46.20
<i>Calanus</i> spp. AF	5.88	3.55	5.33	1.49	10.20	56.40
<i>Eupagurus</i> zoea	3.95	0.56	4.12	1.06	7.88	64.29
<i>Calanus hyperboreus</i> AF	0.23	2.20	2.96	0.39	5.66	69.94
<i>Themisto libellula</i>	2.45	0.00	2.77	0.89	5.31	75.25
<b>Hc2' vs. Kc2'</b>						
Average dissimilarity = 50.22%	Hc1	Hc3				
<i>Calanus</i> spp. CV	27.21	13.89	22.75	1.65	45.30	45.30
<i>Calanus</i> spp. AF	8.66	3.51	7.97	1.43	15.87	61.17
<i>Themisto libellula</i>	1.92	2.49	4.26	0.97	8.49	69.66
<i>Eupagurus</i> zoea	2.54	0.00	3.37	0.92	6.71	76.38

Little auk chicks' diet composition in comparable periods in Hornsund and Kongsfjorden colonies in 2016 (Hc2' and Kc2') also differed significantly (Table 26). A separation of samples from both investigated periods on the nMDS plot was more pronounced than in 2015 (Fig. 44). SIMPER analysis indicated that the average dissimilarity between the diet composition in both study periods in two colonies was also moderately high, and was influenced mostly by *Calanus* spp. CV and *Calanus* spp. AF (Table 25). *Eupagurus* zoea was observed only in samples from Hc2', but contributed substantially less to overall dissimilarity.

Table 26. Results of two-factor multivariate PERMANOVA for the little auk chicks' diet composition in Hornsund and Kongsfjorden in 2016.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$
Colony	1	11455.0	15.607	<b>0.001</b>	24.75

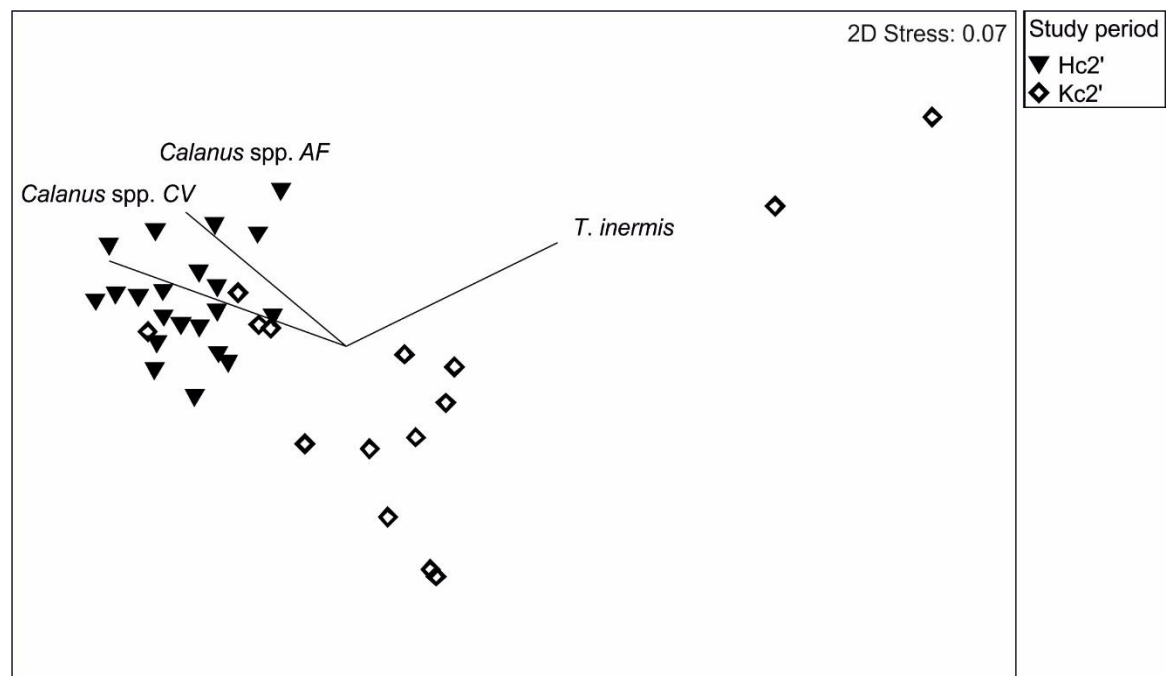


Fig. 44. The nMDS of the little auk chicks' diet composition in Hornsund and Kongsfjorden colony in 2016. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

## Seawater zooplankton samples vs. diet samples in Hornsund

The composition of *Calanus* spp. older copepodite stages (CIV-AF) biomass in seawater zooplankton samples differed significantly from those collected at the same time from little auks (Table 27). The pairwise post hoc PERMANOVA tests indicated that the composition of *Calanus* spp. older copepodite stages differed between seawater zooplankton samples and diet samples in most study periods (H2a vs. Hc1; H2b vs. Hc2; H2' vs. Hc3'). They were very similar in only one comparable study period (H3 and Hc3) (Fig. 45).

Table 27. Results of two-factor multivariate PERMANOVA for the *Calanus* spp. older copepodite stages composition in seawater zooplankton samples and diet samples in Hornsund in 2015 and 2016.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Period	3	719.34	1.4821	0.199	3.3751	
Sample type	1	25627	52.801	<b>0.001</b>	25.611	
Period x Sample type	3	24.177	5.2256	<b>0.001</b>	14.131	H2a≠Hc1; H2b≠Hc2; H2'≠Hc3'

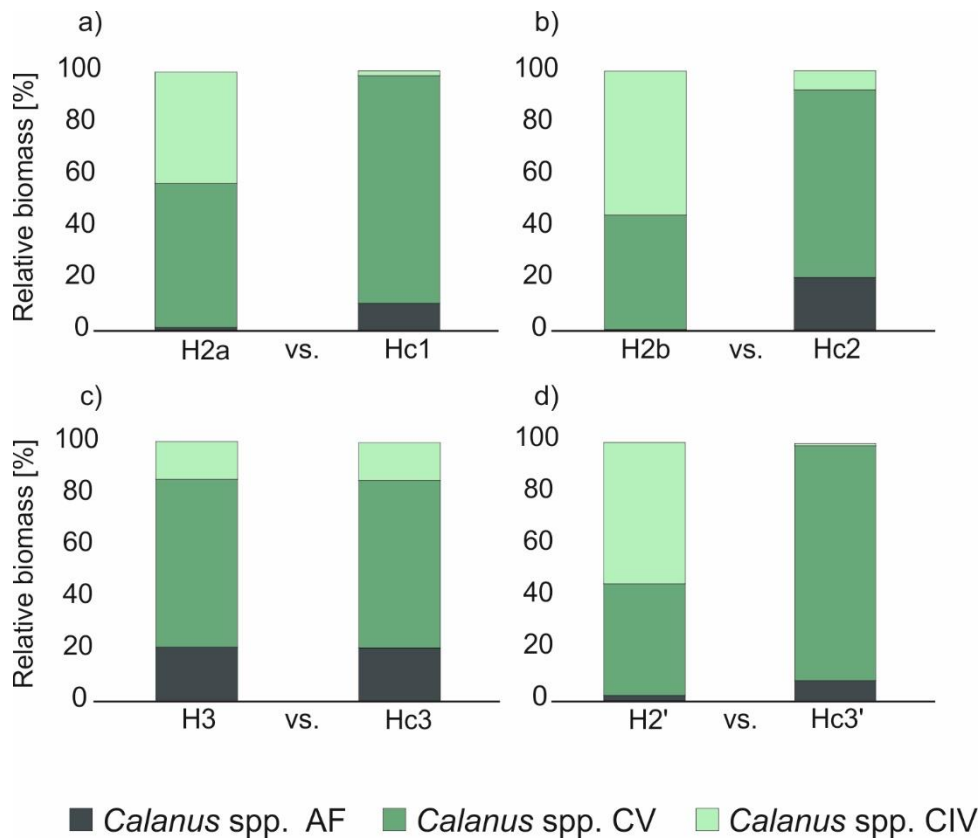


Fig. 45. Composition of *Calanus* spp. older copepodite stages (CIV, CV, AF) in seawater zooplankton samples (H2a, H2b, H3, H2') and diet samples (Hc1, Hc2, Hc3, Hc3') in comparable study periods in 2015 (a, b, c) and 2016 (d) in Hornsund.

### Seawater zooplankton samples vs. diet samples in Kongsfjorden

In Kongsfjorden the composition of older copepodite stages of *Calanus* spp. (CIV-AF) biomass also differed significantly between seawater zooplankton samples and diet samples collected at the same time (Table 28). The pairwise post hoc PERMANOVA tests indicated that the composition of *Calanus* spp. older copepodite stages differed in all comparable study periods (K1 vs. Kc1a, K2 vs. Kc2b, K1' vs. Kc1'a, K1.5' vs. Kc1'b, Fig. 46).

Table 28. Results of two-factor multivariate PERMANOVA for the *Calanus* spp. older copepodite stages composition in seawater zooplankton samples and diet samples in Kongsfjorden in 2015 and 2016.

Factor	df	MS	Pseudo- <i>F</i>	<i>p</i>	$\sqrt{\text{ECV}}$	Pairwise tests
Period	3	227.41	1.0118	0.392	0.49784	
Sample type	1	25627	11158	<b>0.001</b>	24.764	
Period x Sample type	3	24.177	931.19	<b>0.005</b>	11.499	K1≠Kc1a; K2≠Kc2b; K1'≠Kc1'a; K1.5'≠Kc1'b

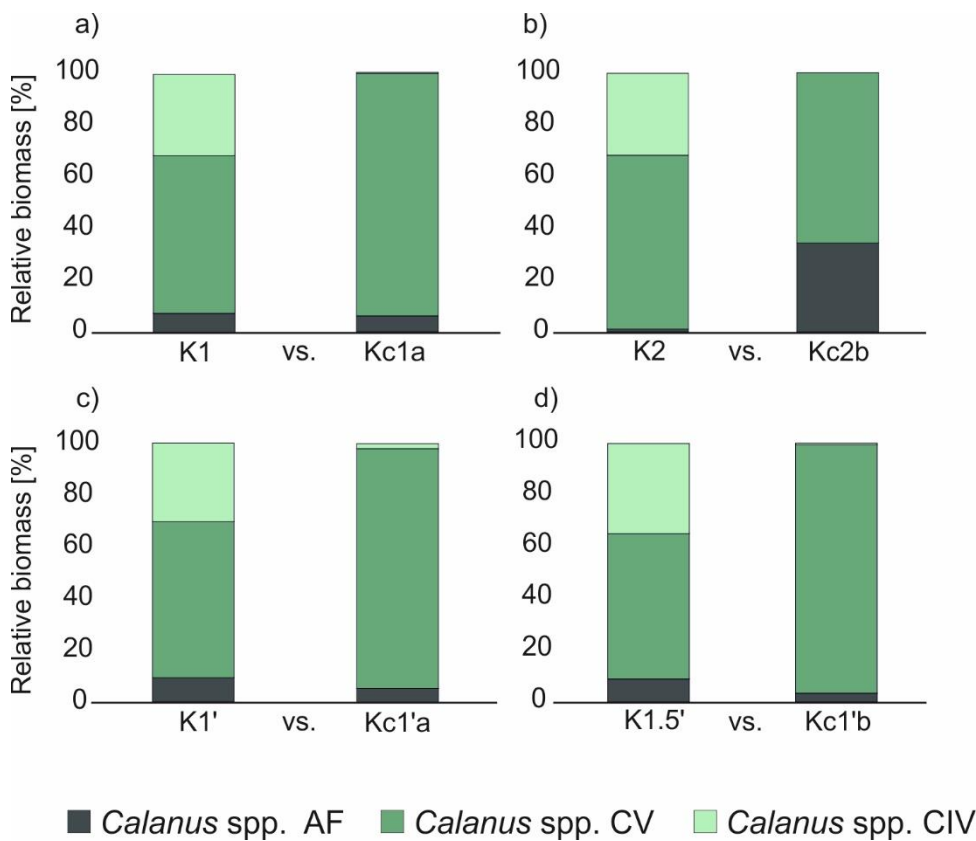


Fig. 46. Composition of *Calanus* spp. older copepodite stages (CIV, CV, AF) in seawater zooplankton samples (K1, K2, K1', K1.5') and diet samples (Kc1a, Kc2b, Kc1'a, Kc1'b) in comparable study periods in 2015 (a,b) and 2016 (c,d) in Kongsfjorden.

## 4. DISCUSSION

### 4.1. THE TWO SIBLING SPECIES OF *CALANUS*

To date, a species-based approach for investigating ecological functions of plankton assemblages was mainly adopted, which emphasized the different life strategies and consequently the different roles of *Calanus glacialis* and *C. finmarchicus* as climate and ecological indicators (Reygondeau and Beaugrand 2011; Wassmann et al. 2011, Falk-Petersen et al. 2007; Kwasniewski et al. 2010). However, this thesis is based on the combined '*Calanus* spp.' category in the light of recent studies indicating that the lipid content is not species-specific feature and that rather the trait-based approach seems to be more appropriate to understand the process of energy transfer to higher trophic levels on a larger scale (Renaud et al. 2018). The additional argument is the fact that the proper recognition between the species is not such straightforward as has been believed for decades. Traditionally *C. glacialis* and *C. finmarchicus* were distinguished by their morphological characteristics (by linking particular copepodite stage with the proper prosome length), however, recent studies using molecular tools have shown that the separation of these two species exclusively on the basis of morphologic criteria without genetic identification is unreliable (Parent et al. 2011; Gabrielsen et al. 2012; Nielsen et al. 2014; Choquet et al. 2018; Renaud et al. 2018). Additionally, some observations of hybridization of both species were noted (Parent et al. 2012, 2015), which may also contribute to hinder their proper identification.

In order to gain a broader view on the *Calanus* population characteristics, in this study individuals of both species were identified and separated in accordance with the traditional morphological classification based on Kwasniewski et al. (2003), by measuring the prosome length. The results have shown that neither the specimens classified as *C. glacialis* nor *C. finmarchicus* were following a normal size distribution. This confirms that the size criterion is not a reliable tool to accurately classify an individual for a given species (Ragonese and Bianchini 1996). Interestingly, contrary to the previous studies, which indicated the dominance of *C. glacialis* in cold water masses of Hornsund area (Kwasniewski et al. 2010, 2012; Gluchowska et al. 2016; Trudnowska et al. 2016), a clear dominance in the number of individuals classified as *C. finmarchicus* was observed in this

dissertation. These interesting premise should definitely be verified in the nearest future by simultaneous morphometrical and molecular analyses.

Such an inconsistency between the observed data and the literature may be explained by the broader size ranges of both species than previously assumed (Parent et al. 2011; Gabrielsen et al. 2012). A right-skewed size distribution of *C. glacialis* sizes both in Hornsund and in Kongsfjorden presented in this dissertation is most probably caused by the fact that larger individuals classified as *C. finmarchicus* are in fact smaller individuals of *C. glacialis*. Renaud et al. (2018) showed with the use of molecular methods that the size range of *C. glacialis* CV starts from almost 2 mm prosome length, which clearly overlaps with the size range of the same development stage of *C. finmarchicus* (i.e. 2.9 mm in case of CV, Kwasniewski et al. 2003). Therefore, considering that about 1/3 of CVs of *Calanus* individuals in the size range of 2.0-2.9 mm (classified morphologically as *C. finmarchicus*) might be in fact *C. glacialis* (Renaud et al. 2018), their real abundance would be significantly underestimated. A similar discrepancy in the separation of species by molecular and traditional methods was observed in three Arctic fjords - Billefjorden, Kongsfjorden and Rijpfjorden, where fifth copepodite stage (CV) of *C. glacialis* individuals were significantly smaller than assumed just by the morphometric classification (Gabrielsen et al. 2012). The ratio of *C. finmarchicus* to *C. glacialis* in Kongsfjorden classified on the basis of morphological identification was 52% to 48%, while genetic identification indicated a ratio of 29% to 71%, respectively, with a significant predominance of *C. glacialis* (Gabrielsen et al. 2012). The overlap of the size ranges of the two species was also observed by Choquet et al. (2018) in four distant regions in the North Atlantic and Arctic Ocean, including the Svalbard Archipelago. Interestingly, in two other regions studied – White Sea and Raunefjord/Korsfjord the two species did not co-occur (Choquet et al. 2018).

The phenomenon of varying size ranges of two species is associated mainly with environmental conditions and oceanic circulation pattern (Parent et al. 2011) and in consequence with their ecology (e.g. the feeding life history, developmental rate, competition; Grigg et al. 1989; Lindeque et al. 2006, Leinaas et al. 2016). In studies conducted in Canadian Arctic and along Atlantic coasts the pronounced size overlap of *C. glacialis* and *C. finmarchicus* occurred mainly in regions that are under the influence of cold Arctic water masses in contrast to only slight overlap in warmer areas (Parent et al. 2011). This agrees with presented dissertation results, because the observed three modes of

*Calanus* size distribution in colder Hornsund region point towards a large size overlap between two species (Fig. 5) contrary to the warmer Kongsfjorden region, where more pronounced size separation between species was observed (Fig. 6).

In the light of the above mentioned issues, to avoid the problem of misidentification of *C. glacialis* and *C. finmarchicus*, these two species had to be combined altogether into one *Calanus* spp. category. This decision was additionally supported by the fact that both *Calanus* species are crucial component of the little auk diet in Spitsbergen (Boehnke et al. 2015; Jakubas et al. 2016a; Boehnke et al. 2017) and that the lipid content, which is the most important in the context of high energy demands of these seabirds (Karnovsky et al. 2003; Jakubas et al. 2007; Kwasniewski et al. 2010) is not species specific, but is related to the body size (Renaud et al. 2018).

## **4.2. RELATION BETWEEN ZOOPLANKTON SIZE AND SEAWATER TEMPERATURE**

Body size is a fundamental biological unit that is closely coupled to key processes at individual, population and community scales (Brown et al. 2004). The individual size of zooplankton is tightly coupled with the ambient seawater temperature, which is known as the temperature-size-rule (TSR; Atkinson 1994; Angilletta et al. 2004). According to TSR ectotherms grow slower, but mature at a larger body size in colder environments. The effect of increasing temperatures on cell and/or body size is observed and predicted over a range of ecosystems, terrestrial and aquatic, and becomes an increasingly relevant problem in the era of climate change (e.g. Gardner et al. 2011).

Organisms are able to reduce their body size in response to warming (Gillooly 2000; Daufresne et al. 2009; Gardner et al. 2011) and the high variability of the body size of *C. glacialis* along its geographical range confirms this statement (Gillooly 2000; Leinaas et al. 2016; Choquet et al. 2018; Renaud et al. 2018). Therefore Banas et al. (2016) predicts decrease in *Calanus* body size along with higher seawater temperatures. In experimental studies on *C. finmarchicus* carried out in laboratory conditions, the prosome length decreased significantly with increasing temperature. However, this relationship was stronger as the species development progressed, so as it was especially well-pronounced in late copepodite stages (Campbell et al. 2001). Such correlation was also true for *C. finmarchicus* and *C. helgolandicus* by Wilson et al. (2015), who found out the smallest



observed prosome length of *C. finmarchicus* (2.4 mm) at a temperature above 10°C, while the largest size (2.6-2.8 mm) was observed mainly at a temperature not exceeding 7.5°C. A similar relationship occurred in presented dissertation, because at a temperature of about 7.5°C the maximum prosome length of the *Calanus* spp. individuals did not exceed 2.8mm (Fig. 7), whereas the largest individuals (>3.5mm) were observed in seawater temperature not exceeding 4°C. Similar observations were noted by Parent et al. (2011), who detected that individuals of *C. glacialis* with the largest average prosome length (3.2-3.5 mm) were recorded after development in water with a temperature not exceeding 3°C. Parent et al. (2011) showed also that the average prosome length of *C. glacialis*, *C. finmarchicus* and *C. helgolandicus* differed spatially in some Atlantic areas and Canadian Arctic due to different environmental conditions.

This dissertation also showed differences in body size of all *Calanus* copepodite stages between two fjords, with smaller prosome length in warmer Kongsfjorden than in colder Hornsund (Fig. 4). Being aware this may be caused by differences in proportions of *C. glacialis* to *C. finmarchicus*, also the change in individual size of particular species has to be taken into consideration, particularly when two hydrographically different regions have been compared. It is especially important in the light of recent studies demonstrating the high size plasticity of *Calanus* (Gabrielsen et al. 2012; Choquet et al. 2018; Renaud et al. 2018) and considering the fact that temperature is a key factor determining body size in copepods (Huntley and Lopez 1992; Campbell et al. 2011).

Environmental conditions, particularly temperature, but also salinity (Trudnowska et al. 2015), have a significant impact on the size structure of zooplankton (Alcaraz et al. 2014; Trudnowska et al. 2014, 2016, 2018; Balazy et al. 2018). The seven-year, high-resolution, optical counter study (2010-2016, Balazy et al. 2018) in the region of the West Spitsbergen Shelf showed a clear relationship between higher share of small zooplankton fraction with higher seawater temperatures. This dissertation also indicated a significant effect of temperature on the mean size of zooplankton community (Fig. 12). At higher seawater temperatures (5-7°C) the mean size of zooplankton community was lower, corresponding to the size of small copepods, while opposite trend was observed concerning lower temperatures. This is in line with previous observations which indicated high concentrations of smaller zooplankton in warmer seawater >6°C (Trudnowska et al. 2016) and the highest proportion of large size fraction in lower temperature ~4°C (Balazy et al. 2018).

### 4.3. DOMINANT ZOOPLANKTON TAXA CO-OCCURRING WITH CALANUS

The key element of zooplankton communities in Svalbard waters are *Calanus* species, especially in terms of biomass (e.g. Daase et al. 2007; Falk-Petersen et al. 2007; Blachowiak-Samolyk et al. 2008; Weydmann et al. 2014), however its percentage in total zooplankton abundance is highly variable in time, space and under different hydrographic conditions as was shown in Hornsund by Kwasniewski et al. (2012). In this dissertation the percentage of *Calanus* spp., in total zooplankton abundance was the highest in Hornsund, while in Kongsfjorden was significantly lower in both studied years (Fig. 11). Similar predominance of *Calanus* spp. in Hornsund contrary to Kongsfjorden was also recorded in 2007 (Gluchowska et al. 2016). Also Trudnowska et al. (2015) found higher proportion of *Calanus* spp. in zooplankton communities in colder Hornsund than in Atlantic-influenced Magdalenefjorden. The smaller percentage of *Calanus* spp. in Kongsfjorden may result from the strong advection of the Atlantic Water carrying with warm-water also boreal zooplankton smaller than larger copepods (Willis et al. 2006, Lischka and Hagen 2016; Gluchowska et al. 2017a). Nevertheless, these studies in accordance with the results of this dissertation indicate the very important role of *Calanus* spp. in the Arctic zooplankton community.

The presence and high abundance of nauplii is in general an important contributor to the secondary production. In this dissertation the presence of Copepoda nauplii mainly reflecting the completing reproduction of *Calanus* spp. at the beginning of summer season since their abundance decreased in time of the study periods. This observation is consistent with natural reproduction pattern of *Calanus* spp. (e.g., Daase et al. 2013).

The abundance of *O. similis* is increasing gradually in Spitsbergen fjords since 2006 (Gluchowska et al. 2016) as a consequence of progressive “Atlantification” of these waters (Gluchowska et al. 2017a). The increasing importance of small copepods in the zooplankton composition (Weydmann et al. 2014) is one of the most spectacular examples of the progressing warming that have already been documented (e.g. Richardson and Schoeman 2004). Due stronger advection of warmer, highly saline waters originating from the lower latitudes (IPCC 2014), the presence and/or increasing share of boreal/North Atlantic species in Arctic zooplankton has been already observed along the west coast of

Svalbard (Berge et al. 2005; Lischka and Riebesell 2012; Bauerfeind et al. 2014; Ormanczyk et al. 2017). *Oithona similis* is relatively numerous taxa along the West Spitsbergen Shelf. Its contribution differs depending on hydrographic conditions (Auel and Hagen 2002; Hopcroft et al. 2005; Daase and Eiane 2007; Madsen et al. 2008; Gluchowska et al. 2016). This dissertation showed relatively high and constant percentage of *O. similis* in total zooplankton community (average approx. 20%) in both studied years and regions. Due to the omnivorous feeding strategy of *O. similis* - this species is more flexible and adapts more easily to difficult, often very rapidly changing environmental conditions (Turner 2004). Such flexible feeding strategy may cause replacement of larger copepods with small ones (Uye 1994; Turner 2004).

Another small copepod *Pseudocalanus* spp., was also an important component of the zooplankton community. Its abundance was minor at the beginning, but increased later in the season in Hornsund. Such increasing abundance was described also in Kongsfjorden (Lischka and Hagen 2005). In this dissertation only slightly higher abundances were noted in the colder Hornsund fjord than in warmer Kongsfjorden which was especially visible in 2016, as in the case of previous observations in these two regions (Trudnowska et al. 2015, 2016; Gluchowska et al. 2016).

Significant differences between the investigated fjords concerned also percentages of other zooplankton groups, e.g. the percentage of *Limacina helicina* veligers and Bivalvia veligers was higher in Kongsfjorden compared to Hornsund. The observed differences in their occurrence in both investigated fjords have been quite frequently reported (e.g., Gluchowska et al. 2016; Ormanczyk et al. 2017). In general, Hornsund is characterized by low abundances of meroplankton (Piwosz et al. 2009, Trudnowska et al. 2014) especially when using typical for sampling mesozooplankton mesh size of 180/200  $\mu\text{m}$ .

#### **4.4. COPEPODITE STRUCTURE OF CALANUS SPP.**

The population structure and reproductive strategies of *Calanus* spp. are highly variable in time and space since both are influenced by strong seasonality in environmental conditions and food supply (Søreide et al. 2010; Daase et al. 2013; Sainmont et al. 2014; Banas et al. 2016; Gluchowska et al. 2017a, 2017b; Espinasse et al. 2018; Renaud et al. 2018). Due to logistical challenges of the high frequency sampling in the Arctic conditions, very few studies regarding monitoring of zooplankton population development have been

published so far (Søreide et al. 2010; Daase et al. 2013; Lischka and Hagen 2016; Bandara et al. 2016; Espinasse et al. 2018).

The copepodite stages development of *Calanus* population followed quite similar trend in Hornsund in both years, however it differed significantly between years (mainly due to the difference between H1 and H1'). In the first study period, the *Calanus* copepodite structure was clearly dominated by young life stages, which coincided with a similar peak in abundance of young stages (~70%) observed in July 2007 in Rijpfjorden (Daase et al. 2013) during pelagic bloom (Søreide et al. 2010). Gradual development of *Calanus* spp. copepodite stages reflected by a dominance of CIV and CV in August and September 2007 in Rijpfjorden (~70%) was also indicated by this dissertation results, where these stages were consequently the most common in the third sampling period (H3 and H3', ~80% and ~90%, respectively). High similarity in the *Calanus* spp. age structure observed in Rijpfjorden and Hornsund indicates a similar timing of reproductive events and its synchrony with ice algae bloom in April and phytoplankton bloom in July (Søreide et al. 2010). In addition, the presence of early stages in all the studied periods might suggest continuous reproduction, or at least, the presence of more than one generation of *Calanus* which is likely in high latitudes (Weydmann et al. 2018; Gluchowska et al. 2017b; Renaud et al. 2018).

In Kongsfjorden, the trend of gradual population development was indicated in this dissertation only in 2015. This observation coincided with seasonal dynamic of *Calanus* spp. population structure emphasised in this fjord as higher contribution of early copepodite stages in July and more advanced population in August by year-round investigation of Lischka and Hagen (2016). In turn in 2016, the age structure was very similar in all three periods (Fig. 16b), which indicates that the population development may vary year by year depending on environmental conditions. Of course this might be due to shorter time intervals between sampling periods in this year but most probably due to different advection impact and consequently seawater temperature regime in Kongsfjorden (Cottier et al. 2005). Temperature difference observed in both years (2°C higher in 2016) together with the advection of younger population from the shelf (Willis et al. 2006) could result in the higher contribution of early stages in 2016. The observed inflow of warmer water masses in K1' (8°C SST, Fig. 47) probably carried younger stages of *Calanus* spp. or young copepodites could represent the offspring of the local population. Individuals advected from the south usually spawn earlier which was indicated by higher proportions of older



vary along with geographical location, but also with temperature and timing of primary production in particular years (Daase et al. 2013; Gluchowska et al. 2017a, 2017b; Ormanczyk et al. 2017; Weydmann et al. 2018). However, the stage composition of *Calanus* spp. followed the same pattern in regions sharing similar environmental conditions, e.g. in the summer (July/August) the high share of early copepodite stages (CI-CIII) of *C. glacialis* was recorded in Svalbard Rijpfjorden and in Canadian Franklin Bay (Daase et al. 2013). Both regions represent similar type of environments with two major bloom events during each year (Forest et al. 2008). Hornsund and Kongsfjorden may differ in terms of *Calanus* spp. population stage composition due to different seasonality in both fjords (Gluchowska et al. 2016; Ormanczyk et al. 2017). Differences in stage composition of *C. finmarchicus* between various localizations both latitudinal and longitudinal in the same year were observed by Gluchowska et al. (2017a, b), and Weydmann et al. (2018). Younger copepodite structure was observed at the northern section crossing West Spitsbergen Current compared to the more southern location and it was also the case in more western areas, towards the older population in the slope region (Gluchowska et al. 2017b; Weydmann et al. 2018). Even if the temperature could be the main factor differentiating *Calanus* stage composition in these regions (Weydmann et al. 2018), the timing of food availability could also play an important role (Gluchowska et al. 2017b). Food supply is known to be the one of the key factors determining adoption of optimal reproductive strategy - capital/income breeder (Varpe et al. 2009; Daase et al. 2013; Sainmont et al. 2014; Banas et al. 2016; Renaud et al. 2018) and the timing of primary production together with strong seasonality were indicated as a key drivers of timing of life history events of *C. glacialis* in different Arctic regions (Søreide et al. 2010; Daase et al. 2013). Although Espinasse et al. (2018) did not observe correlation between *Calanus* phenology and timing of phytoplankton bloom in Svalbard, without taking into account the aspect of food availability, it is not possible to clearly answer the question which factors and to what extent resulted in a different development of *Calanus* spp. in both investigated regions. What is more, *Calanus* may start reproduction before spring phytoplankton bloom using its lipid reserves (Irigoinen 2004; Bandara et al. 2018). With different species/population the level of lipid accumulation also changes (Espinasse et al. 2018), proving the complexity of this issue. Nevertheless, the results of this dissertation together with previous data discussed above provide an evidence that the development rate of



*Calanus* spp. is highly variable in time and space and is tightly driven by the environmental variability which emphasizes the need to continue this type of research.

#### **4.5. FUTURE PREDICTION ESTIMATED BY A SIMPLE CALANUS SPP. POPULATION DEVELOPMENT MODEL**

In the era of dynamic changes observed in the Arctic environment, it is particularly important to predict the future responses of organisms from lower trophic levels that occupy crucial position in marine food web – such as *Calanus* copepods, on which higher trophic levels are highly dependent (Ji et al. 2010). However, due to the complexity of the factors shaping life history and biogeography of *Calanus*, such modeling studies are still challenging (Ji 2011; Ji et al. 2010, 2012; Pierson et al. 2013; Banas et al. 2016; Feng et al. 2018; Renaud et al. 2018).

For the purpose of a wider perspective of this dissertation results, various scenarios of abundance and stage composition of *C. glacialis* and *C. finmarchicus* (treated separately) were described under different temperature conditions, since the two species have different developmental rates and reproduction strategies (Corkett et al. 1986; Madsen et al. 2001, Daase et al. 2013).

For *C. glacialis*, the model showed a prevailing younger copepodite structure in both periods at 3°C compared to 6°C, because of faster development of this species in warmer waters (Corkett et al. 1986). It can be presumed that from little auk's point of view, the warming scenario could be more beneficial due to the higher percentages of late copepodite stages of *C. glacialis*, including CV. However, it should be emphasised that while the abundance of its CVs can be high at 6°C in the second period, it would probably drop dramatically in the third period (Fig. 24). At 3°C, the abundance of CVs would also decrease in the third period however it still will be five times higher compared to 6°C temperature which means that it should cover little auks high energetic demands. Therefore, the slower development of *C. glacialis* at a lower temperature and the presence of CIV in the middle of August makes this species longer available for the little auks when they still need to provide valuable food for their chicks. Møller et al. (2018) found that the long and continuous availability of its prey (*C. glacialis* and *C. hyperboreus*) throughout the entire breeding season is the most important feature determining the selection of breeding area by these birds on Greenland. In the model from this dissertation, the higher CV abundance and

the presence of CIV in the third period at 3°C was caused by the high number of early stages CI-CIII in the second period, a large part of which, due to the relatively low mortality rate (Arnkværn et al. 2005), managed to persist the subsequent 20 days. In turn, the very low CV abundance at 6°C scenario, which is the upper described thermal tolerance for *C. glacialis* (Pasternak et al. 2013; Alcaraz et al. 2014) results mainly from the high mortality rate for the late CIV and particularly CV stages (Arnkværn et al. 2005), which in fact dominated in the second period of this study. Diapause process is also very important for the decreasing trend of older copepodites abundance over time, which in both cases significantly reduced the number of CVs in the last investigated period, when most of these individuals are known to descent to deeper depths (Feng et al. 2018). In Rjippfjorden in August a small part of *C. glacialis* CV was still observed in the upper water column, however the vast majority of the population, ready for overwintering was located at greater depths, mainly 50-100 m (not available for little auks). At the same time in Kongsfjorden all CVs have been indicated at depth below 100 m (Daase et al. 2013). What is more, in September at four Arctic locations Daase et al. (2008) found an increase in the abundance of overwintering stages of *C. glacialis* and *C. finmarchicus* along with depth, with high concentrations at 100-700 m depth stratum. Therefore, based on the results of this model, it can be assumed that a lower seawater temperature conditions allow a larger part of the *C. glacialis* to accumulate sufficient lipid reserves for a winter hibernation and as a result provide their longer availability for little auks in the surface layer (Møller et al. 2018). In turn, according to the warming scenario the highest availability of *Calanus* CV for little auk would be observed much earlier in the season (ca. 2 weeks earlier), while at the end of the breeding season the remaining small part of the CVs may be insufficient. Moreover, due to their high exposition to predatory pressure and high mortality, only a small part of them may be successful to attain their lipid rich overwintering stage and in consequence survive the winter.

*Calanus finmarchicus* as expatriate species in the Arctic Ocean (Conover 1988; Smith and Schnack-Schiel 1990) with population centres located in Norwegian Sea (Hirche and Kosobokova 2007; Falk-Petersen et al. 2009) is well adapted to warmer conditions (Ji et al. 2012; Weydmann et al. 2015; Espinasse et al. 2018). However it also remain sensitive to the increasing seawater temperature, which may lead to phenological shifts (Espinasse et al. 2018; Weydmann et al. 2018) e.g., by changing its dormancy duration (Pierson et al. 2013; Wilson et al. 2016) development rate (Kjellerup et al. 2012; Weydmann et al. 2018)



or seasonal peak (Villarino et al. 2015). In previous studies *C. finmarchicus* has been expected to be transported with Atlantic water masses to the north and not able to reproduce in typical Arctic conditions (Hirche and Kosobokova 2007). Actually it is already known that it successfully reproduces in cooler conditions, so progressing global warming may cause more generations during particular vegetation season (Head et al. 2013; Weydmann et al. 2018). Therefore continuous reproduction of this species during summer has been assumed in the model in this dissertation. Tested model predicts a relatively slow development of *C. finmarchicus* at 3°C, which resulted in the young age structure of the population in both periods. At 6°C the development was so fast that young stages also dominated in both periods. Observed in the warmer Kongsfjorden in the seawater samples in 2016 (this dissertation), the population of *Calanus* was also young throughout the season (Fig. 16b) and due to the assumed additional reproduction (Weydmann et al. 2018) the population in the second period was even younger. However, it developed very fast and as an effect in the last period there was clearly high percentage of CIV which was the most numerous stage at the time. This confirmed potential better adaptation of *C. finmarchicus* to higher temperatures (Weydmann et al. 2015, 2018), because a large part of the population may be able to store sufficient lipid reserves and attain the overwintering stage at the right time of the season (Ji et al. 2012). Additionally, much higher abundances of all stages were observed in warming scenario, which resulted from intensive reproduction (Hirche et al. 1997) and rapid development compared to lower temperatures conditions. However if these new generations of young individuals will have sufficient food supply to develop and overwinter, still remains an open question (Weydmann et al. 2018).

The model described in this study seems to reflect the development of both *Calanus* species in natural environment properly, as it was successfully tested against the real, field data from this investigation. Comparing the results of the stage composition obtained from zooplankton nets sampling carried out during this survey in Hornsund region with the model results, very high coincidence was obtained (Fig. 48).

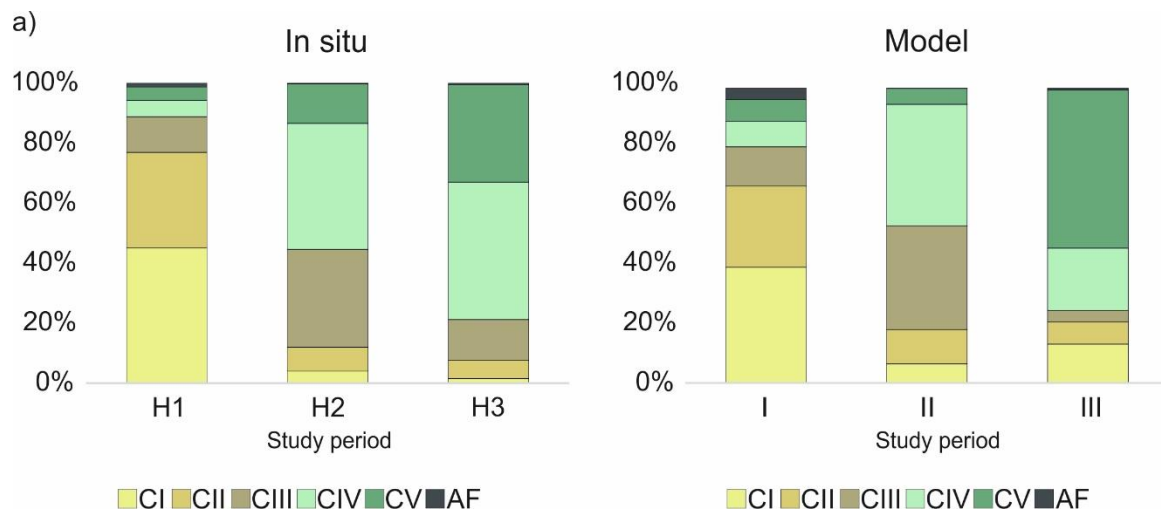


Fig. 48. Comparison of the copepodite structure of *Calanus* spp. in seawater samples in Hornsund 2015 (a) and obtained from the model in 3°C stable scenario (b). The percentage for CIV-AF stages of *C. glacialis* and *C. finmarchicus* in stable scenario were adopted from Gabrielsen et al. (2012) who studied these two species delimitation in Spitsbergen fjords. Since there are no data on the proportion of early stages (CI-CIII) therefore the average proportion of CIV-AF was adopted for them.

However, when interpreting the results of the model in this dissertation, its limitations should also be taken into account. In highly seasonal environments the temperature is one of the main factors determining the development and population dynamics of *Calanus* spp. (Weydmann et al. 2018), however, their food availability is also important (Ji et al. 2012; Banas et al. 2016; Renaud et al. 2018). Furthermore, Banas et al. (2016) in their model showed that the phenology of *C. glacialis* population in a Bering Sea was more dependent on sea ice presence driving the timing of phytoplankton bloom, than on water temperature. In turn, Ji et al. (2012) did not include changes in food availability and ice coverage in warming temperature scenario, which was pointed out by the authors as a limitation of their modelling study. Therefore, because the model described in this dissertation also assumed that potential food for *Calanus* not limited, it may not comprehensively test future *Calanus* population dynamics, in which prey availability and sea ice conditions should be also taken into consideration as varying parameters. However, it should be emphasized that temperature and food supply are often tightly coupled and it is frequently difficult to distinguish between the effects of these two, key factors in similar to this, field studies (Melle and Skjoldal 1998). However in nature, the dynamics of

phytoplankton and protists would rather require the separate, complex model, which was not the scope of this dissertation. The availability of food for *Calanus* is indeed very difficult to quantify, not only because of the high spatio-temporal variability of phytoplankton and protists, but also because of the fact that the *Calanus* diet preferences and possibilities are still not fully recognized, especially in the view of the expected and to some extent also observed changes in their resources. Therefore, it was assumed in the current investigation that the modelling on the *Calanus* development in the warming scenario will be less error-prone if the simulation was based on only one, main factor - temperature. Regarding the model limitations, it has also to be kept in mind that the proportions of the *Calanus* egg production, mortality and descent for winter hibernation were based exclusively on the reference data derived from previous studies, which most probably can also change along with progressing climate warming, and consequently amplify both the modelled conditions and future scenarios. Another obvious limitation of the presented model is the fact that it does not take into consideration zooplankton advection process, especially significant in Kongsfjorden, where it was recently recognized as the important contributor in shaping the local populations of *Calanus* (Basedow et al. 2004; Willis et al. 2006).

#### **4.6. CALANUS SPP. IN RELATION TO ENVIRONMENTAL CONDITIONS**

*Calanus* tend to aggregate in patches, on which little auks are highly dependent (Vogedes et al. 2014; Møller et al. 2018). The high proportion of the preferred prey in zooplankton community makes the victims easily available since they are more visible for visual predators such as the little auk (Stempniewicz et al. 2013). The accessible depth of the prey concentration is also important (Møller et al. 2018). Generally, *Calanus* species concentrate in upper layers during the summer to accumulate lipid reserves from algae for the entire winter (Conover and Huntley 1991; Kosobokova 1999; Falk-Petersen et al. 2009) making them more accessible for planktivorous seabirds. In this dissertation in both regions, the patches with highest percentage of *Calanus* were mainly concentrated within the range of the little auk diving depth (Karnovsky et al. 2011; Amélineau et al. 2016a). The highest percentage of *Calanus* fraction was also similar with the exception of Kongsfjorden in 2016 when only 10-15% was detected. Daase et al. (2013) found the

highest abundance of *Calanus* spp. in July 2007 in Rijpfjorden within 20-50 m depth range indicated as the maximum chlorophyll a concentration.

Although zooplankton organisms have very limited mobility, they are able to concentrate in water masses with optimal conditions (Hirche et al. 2006; Daase et al. 2008; Basedow et al. 2010). Environmental factors significantly shape the distribution pattern of zooplankton in both horizontal and vertical scales, which has been also widely recognized in the Svalbard area (Daase et al. 2007; Błachowiak-Samołyk et al. 2008; Trudnowska et al. 2012, 2014, 2016, Gluchowska et al. 2017; Balazy et al. 2018). This study showed a significant relation between the percentage of *Calanus* in the upper 50 m water layer and the temperature, salinity and chlorophyll fluorescence. Environmental variables explained only 20% of the observed variability regarding the percentage of *Calanus* in both years in the Hornsund region. This might suggest that other important environmental characteristics have not been taken into consideration during the analysis. Vogedes et al. (2014) and Trudnowska et al. (2016) found that the distribution of large copepods tend to be weakly correlated with hydrographic parameters, and that is why they may be more dependent on biological cues rather than oceanographic features. The lack of copepod abundance-temperature relationship was also found by Tande et al. (2000). In turn, Daase et al. (2007) found positive relationship in *Calanus* abundance and hydrographic parameters (temperature and salinity) around Svalbard. Thus, this highly variable phenomenon seems to differ between both *Calanus* species and local populations (Daase et al. 2007). In this study, in Hornsund, the highest percentage of *Calanus* fraction was observed mainly in less saline, cold seawaters with slightly elevated chlorophyll values, so they concentrated mainly in the transition zone between Arctic and Atlantic waters and cold Arctic-type waters (Figs. 29, 31; Balazy et al. 2018). Such consistency in the concentration of *Calanus* in very similar hydrographic conditions in both years, may indicate a habitat selection to some extent, but also to the association to specific water masses or the tendency of plankton to concentrate at the edges of the water currents. In this dissertation in both years the total variability of the percentage of *Calanus* fraction was mainly explained by salinity, which recently was indicated as the most important environmental factor explaining variation in Arctic zooplankton communities (Trudnowska et al. 2015). At shallow locations salinity is even better predictor of *C. glacialis* concentration than temperature (Daase et al. 2007). The process of simultaneous inflow of Arctic and Atlantic waters along the WSS in Hornsund region creates a strong temperature and salinity gradient (Trudnowska et al.

2016; Balazy et al. 2018), which was clearly pronounced in this study (Figs. 29, 31). The various water masses differed also in the phytoplankton concentration, which is frequently associated with temperature gradients (Piwosz et al. 2009) and have a significant impact on vertical distribution of feeding on algae copepods (Leising and Franks 2000; Daase et al. 2008; Trudnowska et al. 2016). The positive relation between *Calanus* percentage and chlorophyll fluorescence was well-pronounced in 2015, when *Calanus* clearly avoided surface layer, substantially depleted with chlorophyll (Fig. 29) and concentrated in chlorophyll-rich subsurface water layers. On the other hand, in 2016 chlorophyll fluorescence peaked in Atlantic water domain, contrary to the distinguished *Calanus* fraction (Fig. 31). Most probably Atlantic-origin population was more developed at that time and thus the older life stages (to which the *Calanus* fraction was restricted) descended to the deeper waters or that only the youngest life stages could actively feed on phytoplankton. Another explanation possible is that the *Calanus* fraction was outnumbered by the extremely abundant smaller zooplankton species (e.g. *Oithona*). In both studied years, the distribution of *Calanus* was only to some extent explained by the temperature, however, the largest patches of *Calanus* were concentrated mainly within seawater temperatures of about 4°C.

In contrast to Hornsund in Kongsfjorden area in both investigated years, seawater temperature was the most important factor influencing *Calanus* distribution and percentage in the total zooplankton. In 2015 the effect of salinity on the variability was minor (explaining less than 1% of variability). *Calanus* seemed not to avoid the low salinity (approx. 33-34) water plume within the surface 20 m along the substantial part of the studied transect. The relationship between temperature and salinity in Kongsfjorden was in opposition to Hornsund region suggesting that in those two very different regions various environmental parameters are shaping the habitat of *Calanus*. In general, the largest patches were observed in the upper water layer in relatively warm water (6-7°C) with lower salinity, just above the patches of high chlorophyll fluorescence. The variability in the community structure of zooplankton in Kongsfjorden is strongly associated with advection (Basedow et al. 2004; Willis et al. 2006, 2008). However the slightly different area of Kongsfjorden sampled might be the reason of such a difference in hydrographical situation between two years. In 2015, the section was designated in the transition zone between inner and outer part the fjord, while in 2016 in the open sea zone of Kongsfjorden foreground. Thus in 2015, the layer of warm water was more distinct and deeper, implying that such a strong

water stratification enhanced probably the *Calanus* concentration within this depth stratum. In turn, in 2016, the layer of warm water was less pronounced and shallower, which may explain why *Calanus* aggregations were restricted only to the very surface water layer. Such a relationship of distribution of *Calanus* patches with warm water masses in Kongsfjorden suggest that they were carried with the inflow of warm Atlantic water. Analogous association was also observed in the Barents Sea (Skjoldal et al. 1992; Tande et al. 2000; Dalpadado et al. 2003; Edvardsen et al. 2003a), where advection is responsible for the largest share of *C. finmarchicus* biomass (Edvardsen et al. 2003b). Additional reason might be differences in the concentration of *Calanus* in two fjords resulted from the different species structure and the predominance of either *C. finmarchicus* or *C. glacialis*. In studies conducted around Svalbard *C. glacialis* abundance decreased with increasing temperature and salinity in shallow areas while it showed opposite trend in deeper, northern waters (Daase et al. 2007). In the same study, *C. finmarchicus* revealed similar pattern in both shallow and deep locations (Daase et al. 2007). However, in the cited above works *Calanus* species were identified on the basis of morphometric differences, thus such assumption may lead to biased results.

#### **4.7. LITTLE AUKS' DIET COMPOSITION VS. FOOD AVAILABILITY**

Numerous studies have shown that *Calanus* spp., comprising *C. glacialis* and *C. finmarchicus*, are the main component of the little auk chicks' diet during summer in Spitsbergen (Wojczulanis et al. 2006; Jakubas et al. 2007; Steen et al. 2007; Karnovsky et al. 2010; Kwasniewski et al. 2010; Wojczulanis-Jakubas et al. 2010; Boehnke et al. 2015; Jakubas et al. 2016a, 2016b) while *C. hyperboreus* is substantial component of chick diets in the eastern (Fort et al. 2010; Karnovsky et al. 2010; Amélineau et al. 2016b) and northwest Greenland (Frandsen et al. 2014; Møller et al. 2018). In turn, the location of the colony and the distance to the feeding grounds differentiate the composition of the supplementary diet components (Boehnke et al. 2017). A part of inter-colony differences in the diet composition result also from bimodal foraging strategy of performing short and long foraging trips by little auk during chick rearing period (Steen et al. 2007; Welcker et al. 2009; Brown et al. 2012; Jakubas et al. 2012). Little auks are known to increase their parental efforts to compensate for poorer feeding conditions (Jakubas et al. 2007, 2011). In

response to high energy demand and lack of suitable preys close to colony they may search for remote areas with productive oceanographic features to forage on larger and lipid rich prey items (Steen et al. 2007; Jakubas et al. 2012, 2013, 2016b; Boehnke et al. 2015).

In this study, in both fjords, it was shown that regardless of the proportion of biomass of late stages of *Calanus* spp. on the potential foraging grounds, little auk consequently foraged mainly on CV stage (~65-90%) and females AF (~8-20%) (Figs. 45, 46). Despite the relatively high availability of CIV, only small percentage of biomass of this copepodite stage was observed in the diet of little auks' chicks in Hornsund, while in Kongsfjorden it was almost absent. Differences between biomass of older *Calanus* stages in diet and in seawater zooplankton from potential feeding grounds were not significant only in the H3 period. This indicates that the timing of high availability of CV in the water match with the period of little auk chicks high food requirements only in Hornsund. What is more, the high biomass of AF, especially in the diet samples from Hornsund was observed even when no AF developmental stage was recorded in the seawater zooplankton samples from birds foraging grounds. Also Steen et al. (2007) observed in Isfjorden that although CIV was the most numerous older *Calanus* copepodite stage on the feeding ground, the little auk almost exclusively selected CV stage. These authors pointed out the significant contribution of AF in food loads, even when females were not detected in seawater zooplankton samples. Møller et al. (2018) also showed underrepresentation of older copepodite stages of *C. glacialis* and *C. hyperboreus* in diet samples from Greenland compared to the *in situ* water samples from their foraging grounds.

Another important in terms of caloric value food item – *C. hyperboreus*, frequently found, but in small numbers in food loads of little auks inhabiting Spitsbergen colonies (Boehnke et al. 2015, 2017) in this study was noted only in one sample from Kongsfjorden. This sample was almost completely filled with this largest *Calanus* species. This extremely lipid rich copepod is usually found in food loads of birds returning from distant foraging grounds located in deep water zone (Pedersen and Falk 2001; Steen et al. 2007). The presence of *C. hyperboreus* in one sample in this study suggests that this bird may foraged in a more distant location than the others (Steen et al. 2007). In turn, a high proportion of *Calanus* spp. (*C. glacialis* and *C. finmarchicus*) in the diet of other birds indicates feeding closer to the colony (Steen et al. 2007). Generally, *C. hyperboreus* occurs more frequently in diet of birds nesting further north (Kwasniewski et al. 2010; Hovinen et al. 2014; Boehnke et al. 2015) probably because of closer distance to the marginal sea ice zone. Even



though *C. hyperboreus* is associated with Greenland waters, it is also often found in seawater samples collected in Kongsfjorden where it occurs in low numbers and deeper in the water column (Kwasniewski et al. 2003, 2013; Walkusz et al. 2009; Gluchowska et al. 2017a; Ormanczyk et al. 2017), thus it may not be accessible for the little auks.

The current study confirmed the important role of *Calanus* spp. in little auk chicks diet in both investigated locations, but the unique ability to switch to completely another prey item in the face of an exceptional change in sea ice conditions was also demonstrated. In Hornsund colony little auk chicks' diet consisted mainly of *Calanus* spp. CV only in the first week of chicks' life. In the second and third week more than 90% of the biomass of almost all samples was dominated by *Apherusa glacialis* - a highly lipid rich ice-associated amphipod (Lønne and Gulliksen 1991; Scott et al. 1999), which occurs in large concentration in locations close to sea ice (Hop et al. 2006; Søreide et al. 2008). More often it is considered as rather supplementary than the main diet component (Fort et al. 2010; Karnovsky et al. 2010; Stempniewicz 2001; Boehnke et al. 2015; Jakubas et al. 2011, 2016a). However, sometimes some part (5-25%) of food loads are almost completely filled with this amphipod (Kwasniewski et al. 2010; Jakubas et al. 2011; Boehnke et al. 2015, 2017), as it was the case in Hornsund in 2004 (Jakubas et al. 2007) and in 2015 (this dissertation). Nevertheless, no previous studies have shown such a high frequency of occurrence of *A. glacialis* in little auks' diet (Fig. 38) as in this thesis. Generally its presence is more expected in the diet of birds nesting further north on Spitsbergen (e.g., Magdalenefjorden, Boehnke et al. 2017), due to the shorter distance to the sea ice edge. Little auks could be foraging on sea ice edge present in this area in August 2015 as observed before by Jakubas et al. (2013) (Fig. 49), while the presence of *A. glacialis* in the diet of birds depends on the ice conditions in a given year (Amélineau et al. 2016b). Extraordinary high frequency of *A. glacialis* in little auks' diet may confirm very high plasticity of foraging strategy of little auks facing variable environmental conditions (Jakubas et al., 2007, 2011, 2014, 2016b; Fort et al. 2010; Grémillet et al. 2012; Hovinen et al., 2014). Little auks are known to adopt flexible foraging behavior in response to various environmental conditions (Amélineau et al. 2016b; Jakubas et al. 2016b, 2017) but the range of this plasticity has not been fully tested yet.



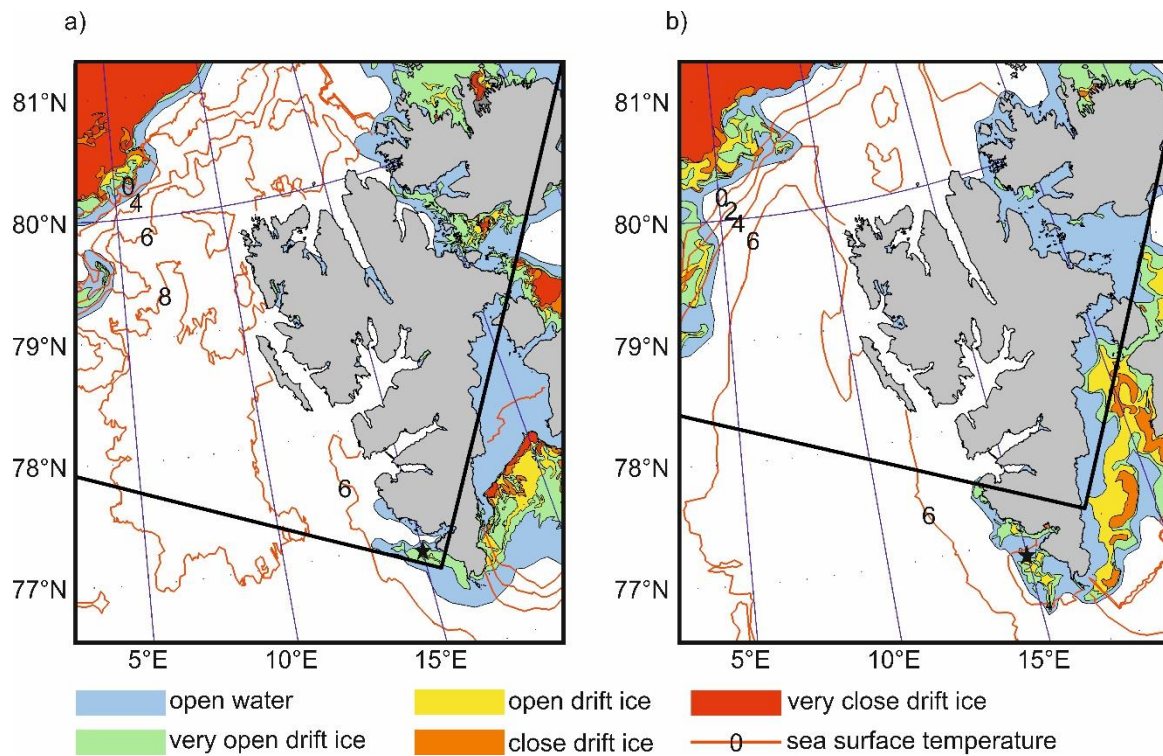


Fig. 49. Sea surface temperature (indicated as numbers on isolines) and sea ice conditions (indicated by colour surfaces) in Svalbard waters in 2015 during Hc2 (a) and Hc3 (b) study periods. Star icon is Hornsund study area. Data source: Norwegian Meteorological Institute.

In this study *Thysanoessa inermis* was another important food item for little auk, especially in Hornsund colony in 2015, where its significant share in biomass (80%) was observed in the first week of chicks' life which is in agreement with previous research from the same region (Boehnke et al. 2015). In other periods, as well as in the diet from Kongsfjorden colony, it was observed rather occasionally since it is regarded as associated with cold Arctic water masses (Hagen and Auel 2001; Boehnke et al. 2015). This species was found more frequently in diet samples from Hornsund colony during warm (42%) rather than cold (35%) seasons (Jakubas et al. 2007). In this study the presence of *T. inermis* was noted only in two out of fifty seawater samples in Hornsund area and in six out of forty six in Kongsfjorden. Generally *Thysanoessa* spp. has been reported, albeit less frequently, in summer diet of little auks in Isfjorden (Steen et al. 2007; Hovinen et al. 2014), Magdalenefjorden (Boehnke et al. 2015, 2017), Aasefjellet (Boehnke et al. 2017); Franz Josef Archipelago (Weslawski et al. 1994), Bjørnøya (Jakubas et al. 2016b), or East Greenland (Harding et al. 2009).

*Pagurus* zoea, the larvae stage of *Pagurus pubescense*, the only hermit crab recorded on Spitsbergen (Balazy et al. 2015) in this study was observed only in food samples from Hornsund colony (Figs. 38, 40) which coincides with previous studies from the same location (Kwasniewski et al. 2010; Boehnke et al. 2015). *Pagurus* zoea is highly abundant in Hornsund region (Boehnke, unpubl.), and despite its low caloric value (Wacasey and Atkinson 1987), it is a frequent component of the diet of little auks foraging near Hornsund (Karnovsky et al. 2003; Fort et al. 2010). Most probably larvae of this species are transported to Hornsund fjord with cold Sørkapp Current (Balazy et al. 2015). Higher abundances and occurrence of this prey item in little auk diet were recorded during colder summer season in Hornsund region (Jakubas et al. 2016b). Another crab larvae – *Hyas* zoea – which noticeably contributed to little auks diet in Hornsund in 2016 usually contributes only slightly to little auk diet (Boehnke et al. 2015; Jakubas et al. 2016b). The occurrence of meroplankton is highly seasonal, coinciding with the reproduction phases of various benthic groups (Kuklinski et al. 2013), thus their contribution to little auks food loads is potentially another example of taking advantage of the existing resources by those seabirds.

Relatively high percentage of *Themisto abyssorum* in total biomass was observed in Kongsfjorden in 2016 (Fig. 42). This amphipod is associated with open-sea waters (Estrada et al. 2012; Gislason and Silva 2012; Boehnke et al. 2017; Dalpadado et al. 2016). Generally, it is a common component of the little auk chicks diet (Steen et al. 2007; Kwasniewski et al. 2010; Boehnke et al. 2017) but its higher frequency of occurrence in this dissertation mainly in Kongsfjorden may be related to well-pronounced impact of warm Atlantic Water (Kraft 2011, 2015). Another representative of this genera – *T. libellula* was observed in little auks' diet from both colonies with the exception of 2015 in Kongsfjorden. Similarly, this amphipod was found to be more important supplementary component of little auk in Hornsund than in Magdalenefjorden colony (Boehnke et al. 2015).

It should be emphasised that the direct comparison of seawater zooplankton with little auk chicks diet is limited because of several methodological problems. One of the most important is active net avoidance of larger zooplankton taxa (e.g., Euphausiacea, *Themisto*) which results in ineffective sampling of these organisms during standard, vertical zooplankton sampling (e.g. Sameoto et al. 1993, 2000; Błachowiak-Samołyk et al. 2017). The other methodological limitation of comparing the zooplankton and diet samples is the

fact that only restricted area of the ocean can be sampled and even if the sampling locations were selected so as to present the 'potential' feeding grounds, some birds will utilize different areas that was not studied due to obvious spatio-temporal cruises limitations.

#### **4.8. MATCH OR MISMATCH?**

Since little auks breeding on Svalbard and Greenland are specialized zooplanktivores focused mainly on *Calanus* spp. (Wojczulanis et al. 2006; Steen et al. 2007; Fort et al. 2010; Karnovsky et al. 2010; Kwasniewski et al. 2010; Wojczulanis-Jakubas et al. 2010; Frandsen et al. 2014; Boehnke et al. 2015; Amélineau et al. 2016b; Jakubas et al. 2007, 2016a, 2016b; Møller et al. 2018), and actually on a specific life stage of this taxon (CV), its survival is at great risk if the climate change progresses. Unfortunately temperature warming has been shown to accelerate the development of *Calanus* spp. (Weydmann et al. 2018), thus the altered phenology of many species has become an increasingly important problem (Stenseth et al. 2002; Jakubas et al. 2016a, 2017) concerning feeding on them higher trophic levels. To date, disturbance in interactions between predators and prey (match/mismatch) have been observed in many groups of organisms, e.g., between fish and plankton (Ottersen et al. 2001; Beaugrand et al. 2003), insects and plants (Visser and Holleman 2001), birds and insects (Winkler et al. 2002; Sanz et al. 2003; Thomas et al. 2001; Visser et al. 2003) shorebirds and arthropods (McKinnon et al. 2012) or seabirds and zooplankton including auklets and copepods (Hipfner 2008; Mackas et al. 2007; Bertram et al. 2017). Negative consequences for offspring was already observed in other birds species which mistimed their reproduction (Perrins and McCleery 1989; van Noordwijk et al. 1995).

Most of the studies on the relationship between *Calanus* occurrence and little auks performance are usually limited to: one region (Steen et al. 2007; Kwasniewski et al. 2012), one year (Steen et al. 2007; Kwasniewski et al. 2010; Jakubas et al. 2015) and low frequency of sampling during one summer season (Steen et al. 2007; Kwasniewski et al. 2010, 2012). Although Jakubas et al. (2016) inferred the plasticity of little auks foraging behavior from Magdalenefjorden and Hornsund in relation to their prey availability, they emphasized that further research with high temporal and spatial resolution is necessary to reliably examine this problem.

The consistent observations, from 2005 (Steen et al. 2007), 2010 (Jakubas et al. 2011), 2015 (Møller et al. 2018) and 2015 & 2016 (this dissertation) confirm that the little auk is able to actively select the preferred prey, regardless of large variations in its availability, which lead to draw positive conclusions about its temporary adaptation. Little auks not only chose older stages of *Calanus* spp., but are able to switch to completely different component of its diet in terms of this preferable food item scarcity. The most high-energy supplementary diet components are associated with cold water masses or directly with sea ice (e.g., *A. glacialis*), which occurs occasionally in the Hornsund area (Jakubas et al. 2007; Kwasniewski et al. 2010), and the northward shift of the sea ice may deprive the little auk of such opportunities (Jakubas et al. 2017). This is particularly disturbing in the perspective of the sea-ice-free summer in the Arctic even by the end of 21st century (IPCC 2014). Despite the high plasticity of the little auks foraging behaviour that has been demonstrated so far (Jakubas et al. 2016b, 2017), it is predicted that it will be threatened by global warming due to the loss of the majority of suitable foraging grounds with the temperature increases of 2°C (Jakubas et al. 2017). Thus it may be forced to limit little auks range occurrence only to areas with high food concentration (Møller et al. 2018). Warming temperatures, providing favourable conditions for breeding, at the same time are causing increasing demand for energy, thus feeding efficiency and reproductive success of the birds largely depends on the quality, abundance and availability of their preferred food (Jakubas et al. 2016). Jakubas et al. (2017) in their model study predict losses of the majority of suitable foraging grounds for little auk at 1-2°C sea surface temperature increase. The results of the model carried out in this dissertation indicate that little auk will face unfavorable conditions at warming scenario since the early development stages of *C. finmarchicus* would dominate. Additionally and despite that the CV would be only available stage of *C. glacialis* at the same time, very low abundances of this stage are expected to be found in the upper seawater layer, available for planktivorous birds. Thus, predicted changes in replacement of large, typically Arctic species (*C. glacialis*) by smaller, more abundant boreal species (*C. finmarchicus*) (Renaud et al. 2018), would not be favorable for the little auk. Even if *C. finmarchicus* is expected to be very numerous at higher seawater temperatures, mainly younger stages would dominate during the little auk breeding period, as shown in this dissertation, which will not be able to deliver the birds high enough energy demands. It will be particularly unfavourable in the light of the latest research showing that little auk is actively targeting larger zooplankters (Enstipp et al.

2018; this dissertation). Such transformation of trophic webs towards smaller zooplankton (Renaud et al. 2018) may temporarily not have a negative impact on the little auk (Amélineau et al. 2016b). However, will little auk start breeding earlier and adjust its optimal timing of arrival (Both and Visser 2001; Jonzén et al. 2007; Møller et al. 2010) to its new prey phenology under changing climate, how long and to what extent it will be able to adapt to these conditions remains still open questions. The predicted reduction in abundance, and consequently the availability of *C. glacialis* at the expense of abundant young population of *C. finmarchicus*, made it possible to define recommendations regarding the use of molecular methods in future research and the need to determine the participation of both species in the diet of the little auks both in the future and on the basis of available historical materials. Correct identification of these two main components of the little auks' diet will allow to better understand the extent of their plasticity to the availability of their preys over the last decades in the dynamically changing Arctic environment.

## 5. CONCLUSIONS

The results obtained in the dissertation have led to the following conclusions:

- The higher variability in *Calanus* spp. copepodite structure was demonstrated in warmer, more advective Kongsfjorden than in colder Hornsund, which indicates the dynamic character of *Calanus* spp. development and their sensitivity to environmental conditions.
- Seawater temperature was confirmed to correlate negatively with both the mean size of mesozooplankton organisms and *Calanus* spp. body length.
- The distribution of *Calanus* spp. was significantly influenced by salinity and temperature, however their significance may vary depending on the region and season.
- The match in time between the state of *Calanus* spp. population development on the little auk foraging grounds and the share of particular copepodite stages in the little auk's diet was better in colder Hornsund than in warmer, less stable Kongsfjorden region .
- Despite high variability in the availability of the late copepodite stages of *Calanus* spp. on the foraging grounds, little auks selected consequently mainly fifth copepodite stage, but they were also able to switch to completely different prey.
- The species-specific model of the *Calanus* spp. development predicted that the seawater temperature increase may lead to a significant reduction in the availability of the late copepodite stages of *Calanus* spp. preferred by the auks, during the period of their highest energy demands. The accelerated development of the Arctic species (*C. glacialis*), can cause a significant shift in time of availability of its fifth copepodite stage in the foraging grounds. The prognosis suggests that the deficit of high-caloric, older copepodite stages is unlikely to be compensated by the sibling Atlantic species (*C. finmarchicus*), since it will maintain mainly the young population in the surface layer of water.



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## 7. FIGURE LIST

**Fig. 1.** Scheme of *Calanus* spp. life cycles. One-year life cycle as commonly displayed by *C. finmarchicus* in ice-free waters; and 1-2 year life cycle as commonly displayed by *C. glacialis*. Copepodite stages – CI-CV; adult females – AF. Solid black arrows: ontogenetic seasonal migration; hatched red and black arrows connect the cycle. Below the bottom axis: abbreviations of the subsequent names of the months comprising one full year starting from January (J). Illustration: Maline Daase.

**Fig. 2.** Map of the study area with current patterns in the Spitsbergen region (simplified from Sakshaug et al. 2009).

**Fig. 3.** Zooplankton sampling stations and bathymetry in two years in Kongsfjorden (a 2015, b 2016, c 2015 & 2016) and Hornsund area (d 2015, e 2016, f 2015 & 2016) marked with circles (first sampling study period K1, K1', H1, H1'), triangles (second sampling study period K2, K1.5', H2, H2') and squares (third sampling study period K3, K2', H3, H3'). The area of Laser Optical Plankton Counter (LOPC) surveys in Kongsfjorden (c) and Hornsund (f) are marked with lines (yellow in 2015, pink in 2016).

**Fig. 4.** Prosome length of *Calanus* spp. copepodite stages: CI (a), CII (b), CIII (c), CIV (d), CV (e) and CVI (AF) (f) in Kongsfjorden and Hornsund. Horizontal black lines shows the median, box represents percentiles, whiskers ranges, dots are values outside the range, red arrows shows statistically significant differences.

**Fig. 5.** Distribution of *C. finmarchicus* and *C. glacialis* fifth copepodite stage (CV) prosome length in Hornsund based on morphological identification. Solid and dotted lines indicate normal distributions.

**Fig. 6.** Distribution of *C. finmarchicus* and *C. glacialis* fifth copepodite stage (CV) prosome length in Kongsfjorden based on morphological identification. Solid and dotted lines indicate normal distributions.

**Fig. 7.** Prosome length of *Calanus* spp. copepodite stages and seawater temperature relationship. Dots represent single individual measured in both fjords. Trendline is marked in red.

**Fig. 8.** Zooplankton community structure and mean size of zooplankton individuals (marked as yellow dots) in Hornsund in 2015 (a) and 2016 (b).

**Fig. 9.** Zooplankton community structure and mean size of zooplankton individuals (marked as yellow dots) in Kongsfjorden in 2015 (a) and 2016 (b).

**Fig. 10.** The nMDS of the zooplankton community structure at particular stations in Kongsfjorden (red) and Hornsund (blue) in: 2015 (a) and 2016 (b).

**Fig. 11.** Comparison of zooplankton community structure in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b).



**Fig. 12.** Relationship between the mean size of zooplankton individuals and seawater temperature. Each dot represents mean size in particular sample. Trendline is marked in red.

**Fig. 13.** The nMDS of the *Calanus* spp. copepodite structure in Hornsund. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

**Fig. 14.** *Calanus* spp. copepodite structure in Hornsund in 2015 (a) and 2016 (b).

**Fig. 15.** The nMDS of the *Calanus* spp. copepodite structure in Kongsfjorden. Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

**Fig. 16.** *Calanus* spp. copepodite structure in Kongsfjorden in 2015 (a) and 2016 (b).

**Fig. 17.** The nMDS of the *Calanus* spp. copepodite structure in Kongsfjorden and Hornsund in 2015 (a) and 2016 (b). Vectors indicate the direction of best correlating variables. Their lengths correspond with the strength of the correlation.

**Fig. 18.** Comparison of *Calanus* spp. copepodite structure in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b).

**Fig. 19.** Copepodite stage index for *Calanus* spp. in Hornsund in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

**Fig. 20.** Copepodite stage index for *Calanus* spp. in Kongsfjorden in 2015 (a) and 2016 (b). Horizontal lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range.

**Fig. 21.** Copepodite stage index for *Calanus* spp. in Hornsund and Kongsfjorden in 2015 (a) and 2016 (b). Horizontal black lines show the median, boxes represent quartiles, whiskers ranges, dots are values outside the range, red arrow shows statistically significant differences.

**Fig. 22.** Modelled abundance of *C. glacialis* copepodite stages (CI-AF) and nauplii (N, solid green line) under 3°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

**Fig. 23.** Modelled abundance of *C. finmarchicus* copepodite stages (CI-AF) and nauplii (N, solid green line) under 3°C seawater temperature scenario. Time interval between study periods (I, II, III) every 20 days starting from 3<sup>rd</sup> July.

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