“Range expansions of scyphozoan jellyfish – the case study of *Periphylla periphylla* and *Cyanea capillata*”

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IV List of Abbreviations

AMOVA	Analysis of Molecular Variance
bp	base pairs
COI	mitochondrial cytochrome c oxidase I gene
D	Actual Differentiation
DNA	deoxyribose nucleic acid
eDNA	environmental deoxyribose nucleic acid
GC-content	guanine-cytosine content
GZP	gelatinous zooplankton
H_d	haplotype diversity value
K2P	Kimura 2-parameter
NCBI	National Center for Biotechnology Information
N_e	effective population size
NJ	Neighbour-Joining
nMDS	non-metric multidimensional scaling
OTU	operational taxonomic unit
PCR	polymerase chain reaction
qPCR	quantitative polymerase chain reaction
RRA	relative read abundance
SD	standard deviation
T_A	annealing temperature
TCS	Templeton, Crandall and Sing
T_M	melting temperature

V Abstract

Jellyfish have been hypothesized to thrive as winners of climate change. Abundances of several jellyfish species are expected to grow, and this could be particularly the case in areas of rapid change, such as the warming Arctic waters. Despite the increased number of reported jellyfish blooms and their negative effects on fisheries worldwide, jellyfish remain an understudied part of zooplankton due to their fragility and their reputation as “trophic dead end”. This study aims to investigate the two scyphozoan jellyfish species *Periphylla periphylla* and *Cyanea capillata*, both of which hypothesized to expand their distribution ranges poleward. The analysis consists of three parts: first, the intraspecific diversity of the two species was investigated using DNA barcoding of samples from Svalbard, Greenland, and Norway. Second, to characterize the status quo of high-Arctic jellyfish species diversity, we applied eDNA metabarcoding of sediment samples around Svalbard. Moreover, the efficiency of this method to reveal pelagic communities was compared with net catches in the same stations. Lastly, species-specific primers were developed and tested, with the future aim to optimize quantitative real-time PCR as a cost-effective and accurate tool for detecting the target species from environmental samples. The study revealed a high intraspecific genetic diversity and a lack of geographic structure in both species. *C. capillata* was shown to consist of three species-level lineages with overlapping distributions, and the cluster identified as *C. capillata* showed a higher genetic diversity than *P. periphylla*. We discussed these patterns of genetic diversity in the light of the life cycles of both species. The metazoan species diversity revealed with the metabarcoding analyses of the Svalbard sediment samples did not represent the pelagic community well, compared to net and trawl catches from the same stations. Many of the zooplankton and especially jellyfish species caught with nets were not represented in the eDNA. Overall, differences in species diversity between the West Svalbard and North Svalbard fjords could be observed, for different metazoan groups, including Cnidaria. In the northern fjords, consistently more cnidarian species were found, indicating the important role jellyfish have in Arctic pelagic communities. We discussed our results with other studies of zooplankton diversity in Atlantic and Arctic waters. The design of a species-specific primer was successful for *C. capillata* on all levels of testing, from tissue DNA extract to environmental samples. Overall, this study shows the importance of investigating jellyfish with modern molecular tools, which may help to inform us on their potential range expansions or population increases in the future. Additionally, we provide guidelines for future research on the topic, based on our study design.

1 Introduction

1.1 A changing ocean – poleward shifts of Atlantic species

Globally, ocean water temperatures are increasing as a direct effect of the anthropogenically induced climate change (IPCC, 2021). Warming ocean temperatures cause a myriad of other changes to the marine environment besides the warming itself, most prominently increased stratification, salinity changes and acidification (Doney *et al.*, 2012). These changes have significant consequences for many organisms and ecosystems (Brierley & Kingsford, 2009; Hastings *et al.*, 2020; Poloczanska *et al.*, 2016; Pörtner & Farrell, 2008). While some organisms may benefit from environmental changes e.g., due to additional availability of food or reduced competition, most organisms will struggle when abiotic conditions shift out of their normal range (Doney *et al.*, 2012; Pörtner & Farrell, 2008). Arctic areas are most affected by climate change, since warming rates are above two times the rate of global warming (IPCC, 2021). An altered abiotic environment means that organisms must adjust to the new conditions according to their physiological needs. This brings about a variety of changes in marine ecosystems, especially in higher latitudes where the changes will be most severe. Since physiological temperature ranges limit the degree to which organisms can adapt, poleward species shifts of temperate species may occur, in some cases displacing endemic Arctic species (Hastings *et al.*, 2020). The warming of Arctic waters and increasing influence of Atlantic waters in higher latitudes (Asbjørnsen *et al.*, 2020; Ingvaldsen *et al.*, 2021), a phenomenon called “Atlantification” (Polyakov *et al.*, 2017), provide new opportunities for cold-temperate species to establish in those regions (Goldsmit *et al.*, 2020; Ware *et al.*, 2014). Poleward shifts have been detected for a variety of organisms, including many zooplankton species, fish, and even marine mammals (Beaugrand *et al.*, 2009, 2002; Fossheim *et al.*, 2015; Kortsch *et al.*, 2015). Along with the predicted species range expansions, the risk of anthropogenically-mediated introduction of non-indigenous species (NIS) is also rising with the increase in human activity and shipping in the Arctic (Goldsmit *et al.*, 2020; Ware *et al.*, 2016). Ballast water and biofouling are important vectors in the transfer of NIS and are only increasing with higher human activities and warmer temperatures, allowing more species to establish in higher latitudes (Ware *et al.*, 2014). In addition to the growing risk of introduction of new species, their establishment in the Arctic is also becoming more common. The increasingly warmer and sea-ice free environment allows boreal species to thrive in higher latitudes, while the environmental conditions for genuine Arctic species deteriorate (Fossheim *et al.*, 2015). Adding to that, the severe changes in food webs and energy pathways also impact the often more specialized Arctic species more than the boreal species, the latter being characterized by broader diets (Fossheim *et al.*, 2015).

1.2 Jellification

The term “jellyfish” includes various phylogenetically different taxa of similar morphology. When talking about jellyfish, typically the pelagic cnidarian medusae of the Hydrozoa, Scyphozoa (“true jellyfish”) and Cubozoa are referred to, along with the ctenophores (“comb jellies”). Gelatinous zooplankton (GZP) is another common term used to describe small, fragile zooplankton species and refers to all abovementioned jellyfish, but also includes other taxa such as pelagic tunicates (e.g., salps, appendicularians) and sometimes, chaetognaths. In recent decades, attention has been brought to increasing abundances of jellyfish biomass in various environments (Brotz *et al.*, 2012; Mills, 2001; Purcell *et al.*, 2007; Richardson *et al.*, 2009). This “jellification” causes wide-ranging effects on ecosystem functioning and services, impacting food-web dynamics and fisheries alike (Roux *et al.*, 2013). Because many jellyfish feed on zooplankton and ichthyoplankton, they are predators and potential competitors of many fish species and if occurring in very high numbers (“blooms”), may substantially decrease fish stocks (Purcell *et al.*, 2007).

It is likely that regime shifts towards jellyfish-dominated food webs are fostered by today’s many anthropogenically induced changes, first and foremost warming ocean temperatures and increased fishing activities (deYoung *et al.*, 2008; Rocha *et al.*, 2015). Ecosystems dominated by jellyfish are characterized as “low-energy” food webs based on flagellates, compared to the diatom-based “high-energy” food webs they might replace (Purcell *et al.*, 2007). In the diatom-based food webs, the zooplankton is dominated by large copepods, which are in turn consumed by fishes. Since the large copepods cannot feed on the small flagellates, the flagellate-based food webs are dominated by small zooplankton which is consumed by the non-size-selective jellyfish (Nagai, 2003). This in turn has profound effects also on the fishery dynamics in those regions, as fishing yields will most definitely decline in low-energy food webs (Purcell *et al.*, 2007). Jellyfish also seem to cope better with extreme climate conditions than fish, in some cases even outcompeting them under such circumstances (Purcell, 2005; Richardson *et al.*, 2009). For example, the scyphozoan jellyfish *Aurelia aurita* and *Rhisostoma pulmo* commonly bloom in the Northern Adriatic Sea and cause severe damage to fisheries in the region, by decreasing the fish stock and interfering with the fishing operations (Palmieri *et al.*, 2014). Another prominent example of jellyfish interference with fisheries is the collapse of the anchovy fishery in the Black Sea, following the introduction of the invasive ctenophore *Mnemiopsis leidyi* (Shiganova *et al.*, 2001).

Typical for jellyfish species is their bloom-forming behaviour, which means they grow to large numbers under favourable environmental conditions over a short period of time (Purcell *et al.*, 2007). Many cnidarians alternate between a sessile, asexual polyp stage and a pelagic, sexual medusa stage (Purcell *et al.*, 2007). This means, that jellyfish population sizes often fluctuate,

making it hard to observe and document longer term changes (Hosia *et al.*, 2014; Mills, 2001). Due to this boom-and-bust population dynamic and the lack of accurate long-term studies on jellyfish abundances, the ocean jellification is still under debate (Condon *et al.*, 2013; Pitt *et al.*, 2018), even though evidence of their impact on ecosystem services and economic activities is accumulating.

1.2.1 Are jellyfish the winners of climate change in the Arctic Ocean?

In the Arctic, reports of rising jellyfish abundances have accumulated in recent years (Brodeur *et al.*, 2008; Crawford, 2016; Eriksen *et al.*, 2012; Lalande & Fortier, 2011; Yaragina *et al.*, 2022), yet there is still a lack of studies describing the magnitude of this phenomenon and its underlying processes (Brotz *et al.*, 2012; Purcell *et al.*, 2007). However, as it seems likely that the ocean jellification is linked to the warming climate and increased fishing activities, we can expect that it will increase in the future, especially in the Arctic (Brotz *et al.*, 2012; Richardson *et al.*, 2009). That the Arctic is changing and will continue to warm is unquestionable (IPCC, 2021), but what the increasing temperatures and sea-ice decline will eventually mean for jellyfish remains unknown until today. Some studies indicate that the warming trend might be favourable for jellyfish productivity, e.g., in the Barents Sea (Eriksen *et al.*, 2012). These warming trends are associated with the ongoing Atlantification, potentially changing the zooplankton composition in the Barents Sea, and therefore altering the feeding conditions for jellyfish. Other studies, for example from the Bering Sea, show that higher temperatures are not necessarily correlated with higher jellyfish biomass (Brodeur *et al.*, 2008). It appears that the links between jellyfish and climate are much more complex and depend on multiple factors such as the survival of early life stages and the type of species in question. Temperate species might benefit from warmer conditions, while species near their temperature limits might perform less well at higher temperatures. To understand how certain species behave under warmer temperatures in the Arctic, we need to know what the communities look like today and how likely they may adapt in the future. For many jellyfish species, especially in the Arctic, those variables remain unknown today.

1.2.2 Periphylla and Cyanea – winners of climate change, but at our expense?

One species that is known to occur in mass abundances is the deep-sea scyphozoan *Periphylla periphylla*, a long-living, predatory jellyfish, that can live up to 30 years (Geoffroy *et al.*, 2018; Tiller *et al.*, 2017). It is negatively phototactic and can survive under various environmental conditions and with extremely low energy intake (Geoffroy *et al.*, 2018; Youngbluth & Båmstedt, 2001). Contrary to other scyphozoans, *P. periphylla* is holoplanktonic: it does not have a benthic polyp stage (Youngbluth & Båmstedt, 2001). The cosmopolitan species typically inhabits the Norwegian, Iceland and Greenland seas, but can also thrive in coastal Norwegian fjords if conditions are favourable (Geoffroy *et al.*, 2018). In fjord systems

it is often bloom-forming and takes on the role as top-predator once a stable population establishes, greatly altering the ecosystem and fisheries (Tiller *et al.*, 2017). Favourable conditions for *P. periphylla* blooms are dim light conditions and limited water exchange, decreasing advection, allowing the photophobic species to build up large abundances in shallower waters (Geoffroy *et al.*, 2018). In the Arctic *P. periphylla* is only rarely reported (Geoffroy *et al.*, 2018), in the northern Barents Sea and in high Arctic fjords (Svalbard). The first documented presence of a *P. periphylla* specimen in a high Arctic fjord (Kongsfjorden, Svalbard) only dates back to 2016 and since then the species increased in numbers at the same location (Geoffroy *et al.*, 2018). Whether this is a sign of a poleward range expansion of the species, or whether the species simply remained overlooked due to limited jellyfish studies in the region is unclear. A northward expansion of the species' range due to climate change is however expected. The low solar irradiances during the polar nights could further enhance the establishment of resident populations of this deep-sea species (Geoffroy *et al.*, 2018). In summer, when the solar irradiances are higher in the Arctic, it is possible that the species actively migrates to greater depths to avoid the light (Geoffroy *et al.*, 2018).

The genus *Cyanea*, consisting of the two species *Cyanea capillata* and *Cyanea lamarckii* are other scyphozoan jellyfish that can often be found in large abundances in the north Atlantic (Hay *et al.*, 1990; Holst & Laakmann, 2014). Of the two species, *C. capillata* is typically described as a northern boreal species, while *C. lamarckii* is typically highly abundant in temperate regions, like the southern North Sea (Barz & Hirche, 2007). These venomous jellyfish are predators of mesozooplankton and other gelatinous plankton (Båmstedt *et al.*, 1994; Liu *et al.*, 2015; Purcell, 2003) but can also be significant predators of fish like the Arctic cod (*Boreogadus saida*) (Crawford, 2016). Like *P. periphylla*, high abundances of *C. capillata* can thus have profound effects on food web structures and higher-level predators like commercially exploited fish species. Hence, they may also impact Arctic fisheries. Similar to other scyphozoan jellyfish, comprehensive studies about abundance and distribution of the genus, in particular in the Arctic are lacking. However, there is evidence that *C. capillata* can dominate zooplankton assemblages in the high Arctic (Geoffroy *et al.*, 2019). Larger aggregations of *C. capillata* can be observed and are increasingly reported on globally (Crawford, 2016; Geoffroy *et al.*, 2019; Hosia *et al.*, 2014; Xian *et al.*, 2005).

Both species considered in this study (*P. periphylla* and *C. capillata*) can significantly influence the trophodynamics in the ecosystems they inhabit (Hosia *et al.*, 2014; Tiller *et al.*, 2017). If present in large abundances, populations of those large scyphozoans can interfere with fish stocks and therefore negatively impact local fisheries. Since it is likely that jellyfish will increase their abundances with globally warming oceans, especially in the Arctic, it is important to study the dynamics of their communities in those regions.

1.3 Novel molecular methods – a chance to study GZP ecology

Since jellyfish are hard to sample with traditional methods, data on their abundance and community structure is often missing, making them largely understudied in many regions, such as the Arctic (Brotz *et al.*, 2012; Licandro *et al.*, 2015; Purcell, 2009). Because GZP is very fragile, small individuals may seep through nets and larger ones being damaged or destroyed, classical net catches and trawls underestimate their abundances (Yaragina *et al.*, 2022) and it is often difficult to find adequate sampling gear (Hosia *et al.*, 2017; Yaragina *et al.*, 2022). Furthermore, GZP is often excluded from zooplankton studies because it was long believed to play a minor role in the food web, being considered a "trophic dead end". To provide a baseline for research on the topic of "jellification", new methods are needed. Advancements in molecular methods have drastically improved the possibilities of studying organisms typically overlooked with traditional methods, like GZP (Bayha *et al.*, 2010; van den Heuvel-Greve *et al.*, 2021). The increasingly cost-effective sequencing technologies allow new insights in jellyfish research. With the growing interest in jellyfish due to the hypothesized jellification, the number of genetic studies on jellyfish is increasing. While still not very common, analyses of connectivity and diversity using genetic markers are starting to become more important (Dong *et al.*, 2015; Iida *et al.*, 2021; Seo *et al.*, 2021).

1.3.1 DNA barcoding – a tool to understand phylogeography

DNA barcoding is a molecular method to identify species by comparing a relatively short genetic fragment, to a reference database of known marker sequences for species identification. Barcoding individuals from separate areas also allows to genetically characterize different geographic populations and study the genetic connectivity between them. The most commonly used genetic marker in animals for this purpose is a fragment of the mitochondrial cytochrome c oxidase I gene (COI), which allows for high enough resolution to effectively distinguish between species, while still being able to show intraspecific variation (Hebert *et al.*, 2003). Its short length (< 1000 bp) and consequential ease of alignment has proven it a suitable marker for barcoding scyphozoan jellyfish (Huang *et al.*, 2008; Ortman *et al.*, 2010). Previous studies showed that the use of COI as a DNA barcode allows identification to the species level, for both *P. periphylla and C. capillata* and can give insight in their genetic connectivity (Lindsay *et al.*, 2015; Ortman *et al.*, 2010).

1.3.2 Genetic connectivity & intraspecific diversity of the studied populations

Since the distribution of *P. periphylla* and *C. capillata* is quite widespread, reaching from temperate to Arctic regions, a high intraspecific diversity between populations from different regions is to be expected. Similar results have been reported for other widespread scyphozoan jellyfish such as the moon jellyfish (*Aurelia* spp.) (Dawson & Jacobs, 2001; Dong *et al.*, 2015;

Ki *et al.*, 2008). Like other zooplankton, populations of jellyfish can be closely linked to the water masses they are found in, and their distributions are often shaped by hydrodynamics (Doyle *et al.*, 2007; Pastor-Prieto *et al.*, 2021; Sørnes *et al.*, 2007). Samples used in this study were taken from five major geographic regions: West Greenland, East Greenland, North Svalbard, West Svalbard, and Norway. Based on previous studies on jellyfish connectivity which show relatively high intraspecific diversities, we want to investigate whether the populations of both target species are genetically diverse and geographically structured. Highly diverse species are more likely to establish in new habitats and thus expand their ranges. Since diverse populations with a large gene pool allow for a high adaptation potential under changing environmental conditions (Pauls *et al.*, 2013), this would add to the idea of jellyfish being climate change winners.

1.3.3 Environmental DNA – an emerging tool for the marine environment

Environmental DNA (eDNA) describes all DNA found in and collected from the environment. It consists of extracellular and intracellular material which can come from dead organisms, shed hair and skin, excreted material, mucus, and faeces (Thomsen & Willerslev, 2015). Sampled material can be analysed in different ways. Whereas DNA barcoding uses DNA from a single species and compares it to a reference, DNA metabarcoding uses DNA derived from an environmental or bulk sample, containing multiple species. A more universal gene is used to include as many species as possible, while still being accurate. Metabarcoding of eDNA makes it possible to screen entire communities by using water or sediment samples (van den Heuvel-Greve *et al.*, 2021). This eliminates the need of sampling individual animals, which can be particularly challenging for gelatinous zooplankton (Purcell, 2009). It also finds the more elusive organisms like jellyfish and other hard-to-sample or even rare organisms. While emerging as a novel tool, eDNA studies are increasingly being applied to the marine environment, but those on jellyfish remain scarce (Ames *et al.*, 2021; Bolte *et al.*, 2021; Minamoto *et al.*, 2017; Ogata *et al.*, 2021). However, combined with other state-of-the-art technologies like *in-situ* video recordings, e.g., from remote operated vehicles (ROVs), they make it possible to give insights on the distribution and role of jellyfish in ecosystems like the Arctic ones, and in which way they are expected to change in the future.

A more targeted approach involves the quantitative polymerase chain reaction (qPCR) using species-specific primers and probes. In a qPCR, a targeted DNA molecule is amplified in a PCR and monitored during the PCR using probes or dyes. This quantifies the genetic material, possibly giving information on relative abundances. For successfully applying a qPCR, species-specific primers need to be designed to amplify DNA from the species of interest only. Once established, this allows for accurate and quantifiable information on the amount of DNA of a specific species in a water or sediment sample. This targeted qPCR approach using

species-specific primers also makes for an effective rapid-detection tool for the species in question. For scyphozoan jellyfish such a rapid-detection tool could be of great interest in many regards. Range expansions due to climate change for species like *P. periphylla* can have dramatic effects on the ecosystems in which they establish large populations (Geoffroy *et al.*, 2018; Tiller *et al.*, 2017). In Norwegian fjords, where *P. periphylla* dominates the community cod fisheries in the fjords have been profoundly impacted (Tiller *et al.*, 2017). Also, aquacultures can be negatively affected by jellyfish occurrences. *C. capillata* is well known to harm aquacultures when its blooms damage whole aquaculture operations (Clinton *et al.*, 2021). Its cnidocytes cause histopathological changes in fish tissues, e.g., harming salmon in aquaculture (Powell *et al.*, 2018). Rapid-detection tools, e.g., utilizing species-specific primers in a qPCR, could help identify jellyfish before they occur in masses and could help to build up precautionary measures.

1.4 Research goal and hypotheses

Since jellyfish have been long hypothesized to be winners of climate change and are likely to increase in numbers especially in new habitats like the Arctic, it becomes crucial to gain information on their genetic composition and their role in the ecosystems. The two large scyphozoans *P. periphylla* and *C. capillata* are known to cause implications on food webs and fisheries when present in large numbers, therefore a tool to monitor their potential range expansions, and detect them in new habitats before they occur in masses, is needed to prevent such events. This study will assess the genetic connectivity of the two species, both of which being hypothesized to expand their distribution ranges poleward, using a set of molecular methods. First, the intraspecific diversity and genetic connectivity of geographic populations will be investigated using DNA barcoding. Second, in order to characterize and compare scyphozoan diversity and structure in different high-Arctic fjords, including our target species, eDNA metabarcoding will be used. Lastly, species-specific primers will be developed to be later used in a qPCR as a cost-effective and accurate tool for detecting the target species in environmental samples.

Considering the large distances between the sampled geographic regions and the environmental differences between them (Atlantic vs. sub-Arctic affinity) we predict some genetic structure between the populations. Because *P. periphylla*'s main habitat seems to be Atlantic waters, populations with Atlantic affinity (East Greenland & Norway) may show higher diversity than those with a sub-Arctic affinity (West Greenland) and may therefore have a higher adaptation potential to climate changes. Populations of *C. capillata* on the other hand, might show higher diversities in sub-Arctic West Greenland, potentially more related to the established populations in the Canadian Arctic, than those in Svalbard, connected to and situated at the margin of the North Atlantic. Owing to previous descriptions of scyphozoan jellyfish populations in Svalbard as well as the descriptions of increased occurrences in the Arctic (Geoffroy *et al.*, 2018), we expect that scyphozoan jellyfish are common in both Arctic and Atlantic-influenced fjords around Svalbard, even dominating the pelagic community. Given the rapid increase of biomass reported in Norwegian fjords and its increasing appearance in Svalbard waters, we suspect that eDNA of *P. periphylla* can be found in other Atlantic-influenced Svalbard fjords, besides the previously described Kongsfjorden population. Lastly, we hypothesize that a newly developed species-specific marker for *C. capillata* and *P. periphylla* will provide a more effective approach for detecting DNA from environmental samples, more specifically sediment samples, than metabarcoding of the same samples using universal primers, as the latter may be subject to amplification and primer biases.

2 Materials and methods

2.1 Genetic connectivity of scyphozoan populations

2.1.1 Sampling of P. periphylla and C. capillata

Adult medusae of *P. periphylla* and *C. capillata* were sampled on three research cruises with the research vessels “Heincke” (HE 560, 18.08.2020 – 04.09.2020 & HE 570, 02.03.2021 – 19.03.2021) (Knust, 2020; Schewe, 2021) and “Walther Herwig III” (WH 440, 05.10.2020 – 23.11.2020) (Werner, 2021)) (**Figure 1**). *P. periphylla* was collected from i) Greenland (WH 440) with 140 µm bottom trawls towed at an average of 3 knots and from ii) Norway (HE 570) using a Maxi-Multinet towed at 2 knots. *C. capillata* was collected from Svalbard (HE 560) using Young Fish Trawls (YFT) and 200 µm and 500 µm towed Bongo nets, including shallow casts (wire length at depth of 20 – 45 m) and deep ones (wire length at depth of 90 – 400 m), with the nets towed at a ship speed of 1.5 – 2.0 knots, a wire speed of 0.3 – 0.5 m/s and a profile time at depth of 30 seconds. From Greenland (WH 440), *C. capillata* was collected with 140 µm bottom trawls, towed at an average of 3 knots. After sorting, specimens were photographed, measured and frozen at either - 80 °C or - 20 °C. Specimens of both species were also collected with a handnet from the wharf in Ny-Ålesund, Svalbard during an AWIPEV research stay (KOP-183, 12.01.2022 – 09.02.2022). A table with all sampling information is included in the appendix (**Appendix 1**).

In the laboratory at AWI, all individuals were defrosted at room temperature, aliquoted in 96 % ethanol and stored refrigerated at 4 °C until DNA extraction. Pigmented tissue, i.e., dark red (*P. periphylla*) or dark brown (*C. capillata*) was dissected in small pieces (aliquots), as these tissues are known to yield a better DNA concentration after DNA extractions. The tissues were sampled from inside the bell of the animal to avoid contamination with DNA from other species caught within the same net.

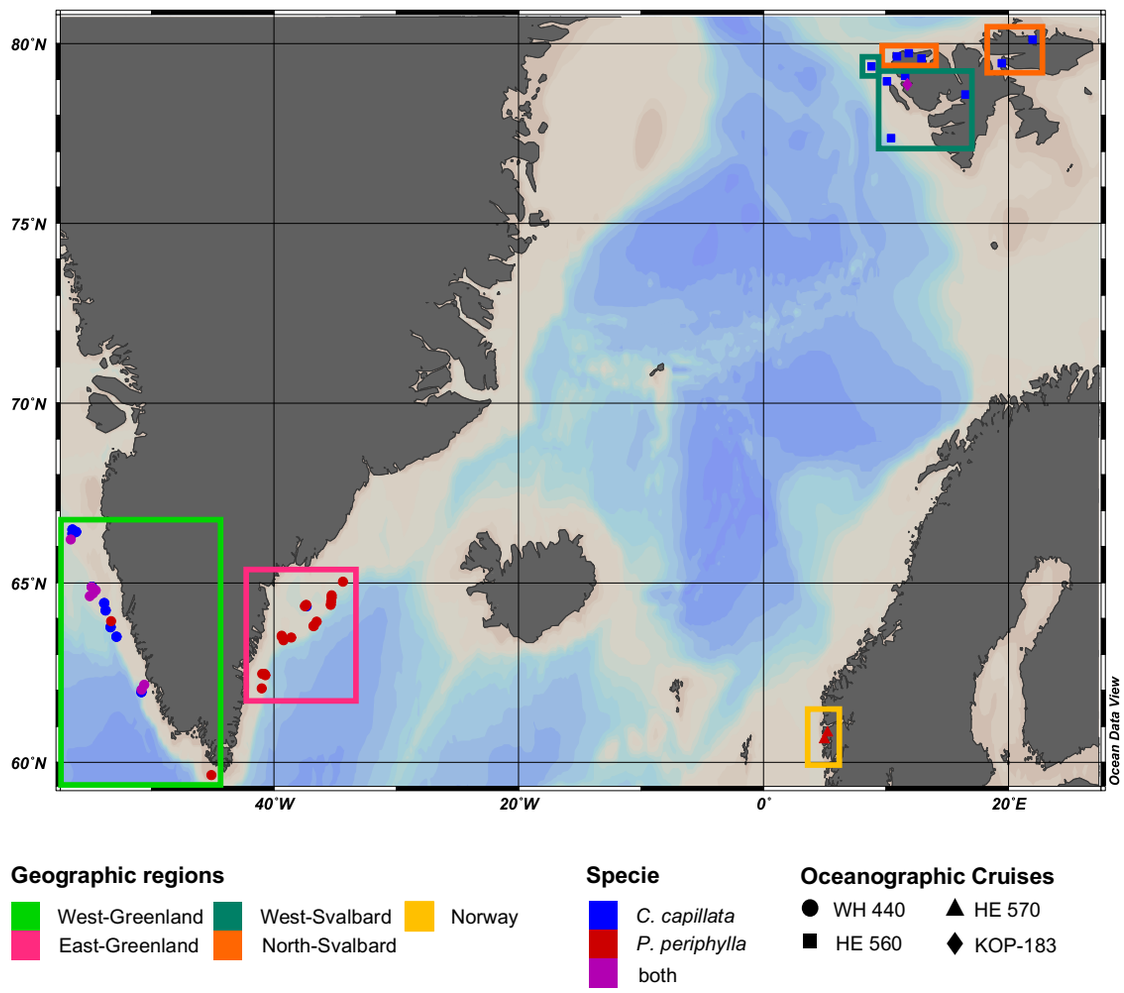


Figure 1 Sampling locations for *C. capillata* and *P. periphylla*. Coloured shapes indicate stations on different oceanographic cruises. Coloured boxes indicate major geographic regions.

2.1.2 DNA extraction of tissue samples and Barcoding

The sampled individuals of *P. periphylla* and *C. capillata* were barcoded for the mitochondrial cytochrome oxidase I gene (COI), which has been used successfully for species identification and genetic connectivity studies for both species (Abboud *et al.*, 2018; Hotke, 2015).

DNA of the adult medusae of *P. periphylla* & *C. capillata* was extracted using the DNeasy® Blood & Tissue Kit (Qiagen, Germany) after the manufacturer's protocol for purification of Total DNA from Animal Tissues. For the extractions, aliquoted and in ethanol (96 %) preserved material taken from inside the bell of the sampled individuals was used. After extraction the isolated DNA was quantified using a NanoDrop™ 1000 Spectrophotometer (Thermo Fisher Scientific, Wilmington, Delaware USA), amplified in a Polymerase Chain Reaction (PCR), and sent to be sequenced (Eurofins Scientific, Germany). For the *Cyanea* samples the universal metazoan primer pair HCO2198 and LCO1490 (Folmer *et al.*, 1994; hereafter called "Folmer-primers") was used for amplification in a PCR and subsequent Sanger sequencing (Eurofins,

Germany). The PCR master mix contained 1-fold HotMaster® Taq buffer (10-fold stock, QuantaBio), 0.2 mM dNTP (2 mM stock), 0.5 µM of each primer (100 µM stock), 0.02 U/ µL 5prime HotMaster® Taq polymerase (QuantaBio) (5 U/µL stock), 3 µL of 10 ng/µL DNA and water for a total reaction volume of 25 µL. Because test PCRs with the Folmer-primers and the specifically for Anthozoa designed primer pair AnthoF1 and AnthoR1 (Hotke, 2015) failed to successfully amplify *P. periphylla* DNA, the primer pair mlCOIintF-XT and jgHCO2198 (Leray *et al.*, 2013); hereafter called "Leray-primers") was used for all specimens of the species. The PCR mastermix for the Leray-primers contained 10 µL 2x AmpliTaq Gold™ 360Master mix (Thermo Fisher Scientific, Wilmington, Delaware USA), 0.16 µL Bovine Serum Albumin, 1 µL of each primer (5 µL stock), 1 µL of 10 ng/µL DNA and 6.84 µL water for a total reaction volume of 20 µL. The PCR conditions for the two primer pairs are presented in **Table 1**. Isolated DNA and PCR products were stored at - 20 °C until further analysis. PCR product of all samples was set to be Sanger-sequenced with an ABI-sequencer (Eurofins Scientific).

Table 1 PCR conditions for amplifying the COI gene using the (a) Folmer-primers and (b) Leray-primers.

(a)			**(b)**		
94 °C	2 min		95 °C	10 min	
94 °C	20 sec	36 cycles	94 °C	1 min	35 cycles
42 °C	20 sec		45 °C	1 min	
65 °C	1 min		72 °C	1 min	
65 °C	16 min		72 °C	5 min	
6 °C	∞		6 °C	∞	

2.1.3 Phylogeographic analyses

Sequences (*C. capillata*: N = 52; *P. periphylla*: N = 88) were manually checked for stop codons, ambiguous base calls, and amino acid translations, in order to avoid the use of pseudogenes, using CodonCode Aligner (CodonCode Corporation, www.codoncode.de). ABI-files were qualitatively checked and merged to align forward and reverse reads. Primer sequences were trimmed from both reads. The consensus sequences were exported as fasta-files and aligned with CLUSTAL-W (Thompson *et al.*, 1994) with COI sequences retrieved from public databases (NCBI GenBank; Bethesda, 2008) in MEGA 11 (Kumar *et al.*, 2018; Stecher *et al.*, 2020). Lists with all COI sequences mined from GenBank are included in the Appendix (**Appendix 3, Appendix 4**). Neighbour-joining (NJ) trees were constructed in MEGA 11 (Kumar *et al.*, 2018; Stecher *et al.*, 2020), based on the Kimura 2-parameter (K2P) method with pairwise deletion and bootstrap support (*N* reps = 2000). GenBank sequences (N = 61, **Appendix 3**) were included in the construction of the *C. capillata* NJ-tree. Intraspecific diversity was estimated using standard diversity indices: number of haplotypes (H), number of

segregating sites (S), haplotype diversity (h), nucleotide diversity (π) number of parsimony informative sites and average number of nucleotide differences (*K*). Diversity indices were calculated in DnaSP 6 (Rozas *et al.*, 2017). To explore the relationships between identified haplotypes, haplotype networks of *C. capillata* and *P. periphylla* were created using PopART (version: 1.7; Leigh & Bryant, 2015), using the Templeton, Crandall and Sing (TCS) method (Clement *et al.*, 2002), based on the maximum parsimony algorithm. Sequences shorter than 658 bp (*C. capillata*, using Folmer-primers) or 313 bp (*P. periphylla*, using Leray-primers) were included in the construction of the NJ-trees but excluded from all other analyses to avoid base-pair loss in longer sequences. To test for hierarchical population genetic differentiation, Analysis of Molecular Variance (AMOVA) was used (Excoffier *et al.*, 1992). Pairwise *D* values were calculated to estimate the genetic connectivity between geographical regions. AMOVA and pairwise *D* were calculated in RStudio (version 2021.09.1) in the R environment (R version 4.1.2) using the packages *poppr* (version: 2.9.3; Kamvar *et al.*, 2015), *mmod* (Winter, 2012) and *apex* (Jombart *et al.*, 2020).

2.2 Scyphozoan diversity in Arctic fjords

2.2.1 Sampling of eDNA sediments

Sediment samples for environmental DNA (eDNA) analyses were collected during the HE 560 “Heincke” cruise in summer 2020 from ten stations around Svalbard (**Figure 2**) using the Mini-corer or Van Veen grabs. Sediment was stored frozen at - 80 °C until further analysis. A detailed overview of the samples is included in the appendix (**Appendix 2**)

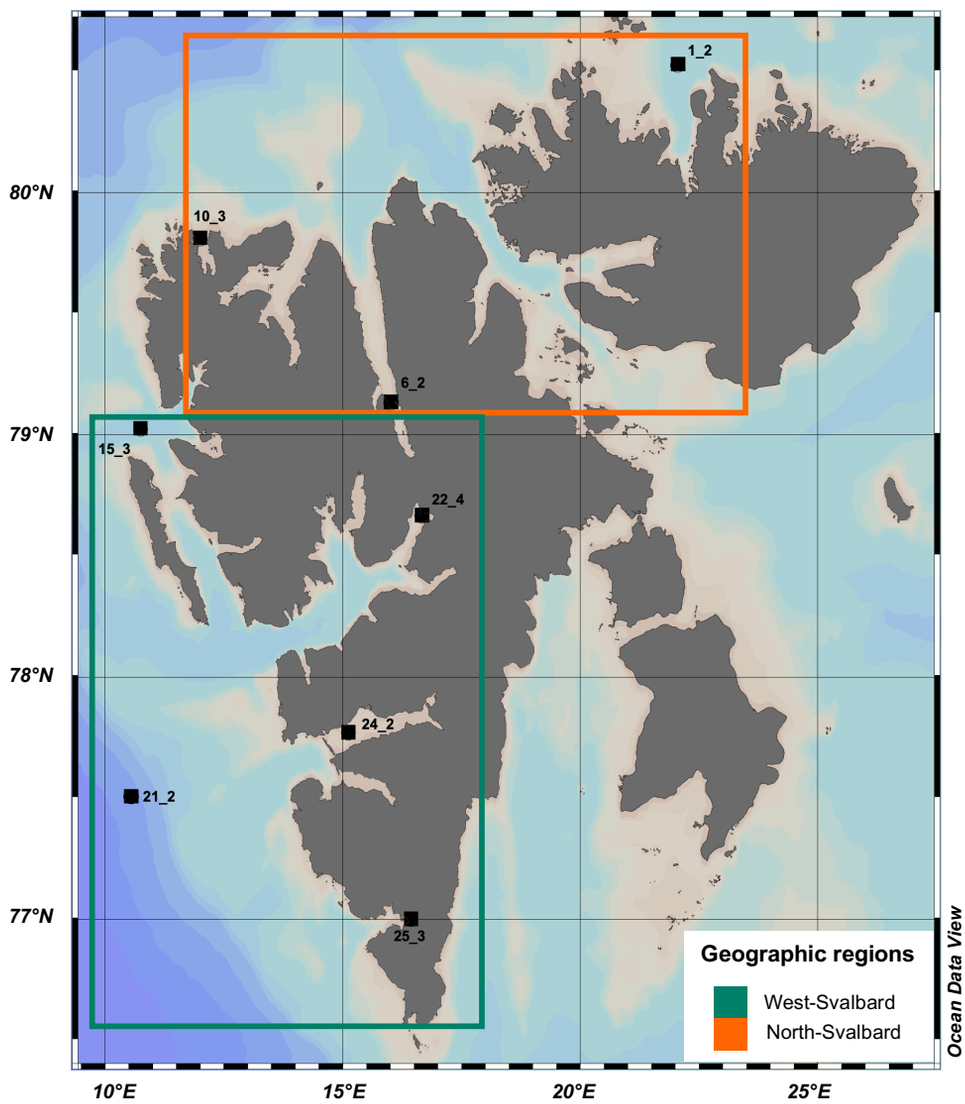


Figure 2 Sediment sampling locations from the oceanographic cruise HE 560. Black squares indicate sampling stations. Coloured boxes indicate major geographic regions.

2.2.2 eDNA extraction and metabarcoding

eDNA was extracted using the DNeasy® PowerSoil Pro kit (Qiagen, Germany) after manufacturer’s protocol in the AWI eDNA laboratory (by Ayla Murray). For amplification in a

PCR and subsequent sequencing using Illumina NovaSeq the Leray-XT primers (Wangensteen *et al.*, 2018) were used to amplify the “Leray-fragment” of the COI gene (Leray *et al.*, 2013), since it has been proven to be an effective marker for investigating metazoan diversity from bulk samples (van den Heuvel-Greve *et al.*, 2021; Leray *et al.*, 2013). After extraction the isolated eDNA was quantified using a NanoDrop^{TM} 1000 Spectrophotometer (Thermo Fisher Scientific, Wilmington, Delaware USA) and amplified with a PCR. For the amplification, AmpliTaq Gold DNA polymerase (Thermo Fisher Scientific, Wilmington, Delaware USA) was used, with 1 µL of each primer (5 µM), 3 µg of bovine serum albumin and 10 ng of DNA in a total volume of 20 µL per sample. The PCR was run for 10 min at 95 °C, 35 cycles of 94 °C for 1 min, 45 °C for 1 min and 72 °C for 1 min, and 5 min at 72 °C. After PCR the amplifications were checked by electrophoresis in agarose gels. PCR products were purified using Minelute PCR purification columns (Qiagen, Germany). The Illumina library was built using the Metafast protocol and sequenced on an Illumina NovaSeq platform (Fasteris SA, Plan-les-Ouates, Switzerland). Library preparation for the sequencing was done by Ayla Murray at the Arctic University of Tromsø (UiT), Norway, in the research group Genetics of Prof. Kim Praebel with assistance of Dr. Owen Wangensteen.

2.2.3 Bioinformatics

The bioinformatics pipeline was conducted following the UiT MJOLNIR pipeline (https://github.com/uit-metabarcoding/MJOLNIR/blob/main/README.md) in the R environment, based on OBITools software suite (version 0.1.0; Boyer *et al.*, 2016). Initially, paired-end reads were aligned using *illuminapairedend*. Demultiplexing, which removes the primer sequences, was done with *ngsfilter*. Length filtering with *obigrep* was performed to only allow sequences between 299 bp and 320 bp and without ambiguous positions. Chimaeric sequences were removed on sample-by-sample basis using the uchime_denovo algorithm implemented in VSEARCH (version 1.10.1; Rognes *et al.*, 2016). Sequences were clustered into OTUs (Operational Taxonomic Units) using the SWARM algorithm (Mahé *et al.*, 2014; 2015), based on linkage-networks created by step-by-step aggregation. Singletons were removed before the clustering step. Taxonomic assignment of the OTUs was done against a local refence database, based on GenBank sequences and provided by Dr. Owen Wangensteen. Pseudogenes were removed with the LULU algorithm. Lastly, sequences were filtered to remove relative read abundances below 1/50000 for every sample and absolute abundances below 2 reads. Prokaryotic sequences were removed since they are considered to be contaminants. Additionally, *Homo sapiens* and Insecta sequences were omitted from the final dataset as well as OTUs originating from tag-jumping of other libraries sequences at the same time (Bathryraja, Amblyraja, Mytilus, *Aglantha digitale*).

2.2.4 Statistical analyses

Statistical analyses were carried out using TaxonTableTools (Macher *et al.*, 2021) in Python (version: 3.10). The sample replicates of the dataset were merged. After calculation of basic statistics including average and total reads per sample, number of OTUs and species per sample, the control samples and OTUs unassigned to the phylum level were excluded.

Relative read abundances (RRAs) were calculated for each station at the phylum and class level. RRAs were displayed in bar charts and Krona charts (Ondov *et al.*, 2011) to illustrate the role of Cnidaria. Rarefaction curves were created to indicate differences in the recovered species richness at the different stations. To assess the differences in community structure between Atlantic-influenced (West Svalbard) and Arctic-influenced (North Svalbard) fjords, non-metric multidimensional scaling (nMDS) was used. To determine the best fit for the dimensions (k), stress was calculated within the nMDS model and plotted over the dimensions. As threshold 0.2 stress was used for finding k, according to (Clarke, 1993). Since the first dimension below the threshold was 2 (**Figure 3**) k = 2 was used for the nMDS model.

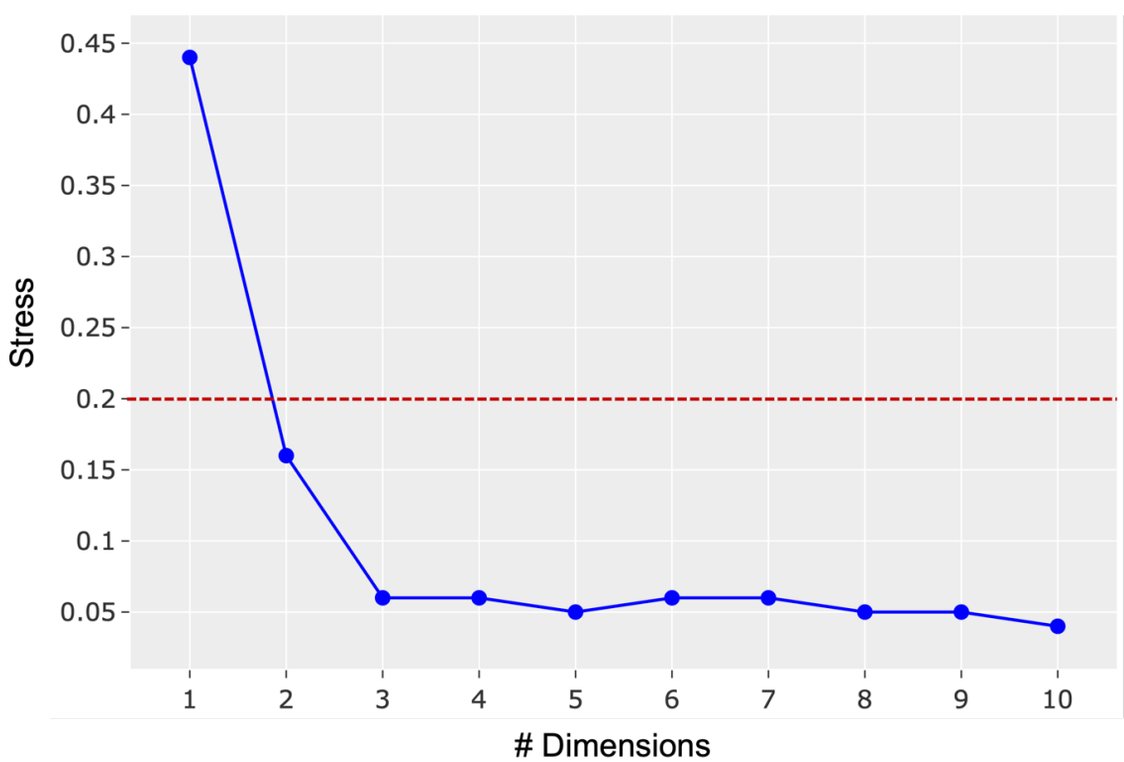


Figure 3 Screeplot of all sediment eDNA samples, plotting stress over dimensions. The red line indicates the threshold of 0.2.

2.3 Species-specific detection of scyphozoans

2.3.1 Primer design

To test and design species-specific primers for the two species *C. capillata* and *P. periphylla*, the target gene COI was chosen, as it is the most widely used gene used for barcoding of metazoan species and thus a large database of reference sequences is available.

All available sequences from the present study (barcoding) and public databases (NCBI GenBank, Bethesda, 2008) for both species were compiled and aligned with CLUSTAL-W (Thompson *et al.*, 1994) in MEGA 11 (Kumar *et al.*, 2018; Stecher *et al.*, 2020). Additionally, closely related species were included in the alignment to later test for non-target amplification. *Atolla* spp. is a genus within the Coronatae order, to which *P. periphylla* belongs. *C. lamarckii* is phylogenetically the closest described sister species to *C. capillata*.

For each species, eight primer pairs were designed using the primer design tool in Geneious Prime® (version 8.1.9; www.geneious.com). The parameters were set as follows: amplicon length between 50 and 150 bp, melting temperature (T_M) between 56 and 58 °C with an optimum of 57 °C, primer optimal temperatures should not differ more than 2 to 5 °C, annealing temperature (T_A) no more than 5 °C below T_M (> 47 °C) and GC-content between 40 and 60 %.

2.3.2 In-silico testing

The primers were tested for specificity against the previously identified non-target sequences using the built-in specificity testing tool in Geneious Prime® (version 8.1.9; www.geneious.com), as well as using the NCBI BLAST® search (Altschul *et al.*, 1990) and Primer-BLAST tool (Ye *et al.*, 2012) to check the primer sequences against the NCBI GenBank database (Bethesda, 2008). To validate T_M, T_A, and GC-content, the IDT OligoAnalyzer™ Tool (Integrated DNA Technologies, Inc.) was used. Additionally, self-dimer formation, primer-dimer formation and hairpin T_Ms were checked using the IDT OligoAnalyzer™ Tool (Integrated DNA Technologies, Inc.).

For each species the three best fitting primers were selected, taking into consideration the likelihood of forming hairpins, self-dimers, and primer dimers, as well as having properties as closely to the selected parameters in the design process. The three selected primers were ordered for *in-vitro* testing (biomers.net GmbH).

2.3.3 In-vitro testing

In the wet lab, the primers were tested on DNA extract from tissue of the target species using standard PCR to verify amplification of the target sequences. Additionally, DNA extract of non-target species (*Atolla* spp., *C. lamarckii*) was used in following PCRs to test the primers for specificity. The PCR mastermix for the newly designed species-specific primers mirrored the mastermix of the Leray-primers and contained 10 µL AmpliTaq Gold™ 360Master mix (Thermo Fisher Scientific, Wilmington, Delaware USA), 0.16 µL Bovine Serum Albumin, 1 µL of each primer (5 µL stock), 1 µL of 10 ng/µL DNA and 6.84 µL water for a total reaction volume of 20 µL. The PCR conditions were: 2 min at 94 °C, 35 cycles of [20 s at 94 °C, 10 s at 55 °C, 20 s at 65 °C], 15 min at 65 °C and a final temperature of 6 °C. Amplification success was assessed using electrophoresis on a GelRed-stained, 3 % agarose gel.

2.3.4 In-situ testing

Since no species-specific primer could be designed for *P. periphylla*, the *in-situ* testing was focused solely on *C. capillata*.

2.3.4.1 Water samples

To test the primers for their specific use on eDNA samples, which have much less concentrated DNA than tissue samples, an eDNA mesocosm experiment was prepared (**Figure 4**). Approximately 20 mg of frozen *C. capillata* tissue was submerged in 10 L of 32 PSU RASalt artificial seawater (Aquacultur Fischtechnik GmbH, Nienburg, Germany) at 2 °C room temperature, to mimic Arctic conditions. After 2 hours, 100 mL water was manually filtered through Sterivex™ sterile filter units (Merck KGaA, Darmstadt, Germany) using 10 mL Omnifix® single-use syringes (B. Braun Melsungen AG, Melsungen, Germany). Samples were taken in triplicates. Before adding the jellyfish tissue, 100 mL artificial seawater was filtered, which was used as a negative control. The Sterivex™ filters were stored at - 20 °C until further analysis. DNA was extracted from the Sterivex™ filters using the DNeasy® Blood & Tissue Kit (Qiagen, Germany) following the protocol by Merten *et al.* (2021). The extracted DNA was then used to test the primer pair in a PCR following the same protocol as in the *in-vitro* testing.

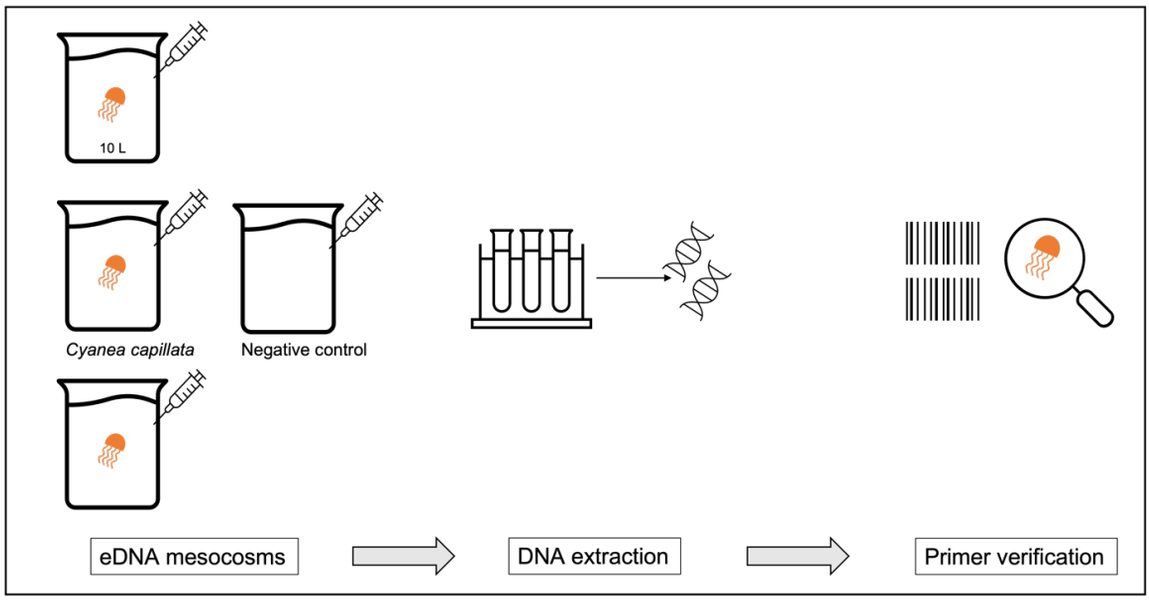


Figure 4 Schematic structure of the eDNA mesocosm experiment. 20 mg tissue of three *C. capillata* samples were submerged in 10 L artificial seawater (2 °C) for 2 h. 100 mL water was filtered from each mesocosm (in triplicates) and one negative control, and DNA extracted from the filters. The DNA extract was then used to test the newly designed species-specific primers.

2.3.4.2 Sediment samples

Lastly, the primer pair designed for *C. capillata* was tested on sediment samples from around Svalbard (HE 560, **Figure 2**). A PCR was performed with DNA extract from the sediment samples following the previously mentioned PCR protocol of the *in-vitro* testing.

3 Results

3.1 Genetic connectivity of scyphozoan populations

The COI sequence data from *C. capillata* resulted in an alignment length of 658 bp, while the sequence data from *P. periphylla* which was obtained from the shorter Leray-fragment resulted in an alignment length of 313 bp. A total of 52 *C. capillata* specimens and 88 *P. periphylla* specimens were sequenced. Respectively, 52 and 70 of those were used in subsequent analyses. The COI barcoding confirmed morphological identification of all sequenced *P. periphylla* specimens (**Figure 5**B). Only one cluster with high bootstrap support (96) can be found within all *P. periphylla* sequences (K2P distance = 0.61 %), comprising specimens from Svalbard (PerZ002, PerZ006, PerZ010) and Norway (Ppe02, Ppe03, Pp313, Ppe19, Ppe26, Ppe46, Ppe51, Ppe53). For the barcoded *C. capillata* specimens, three clusters were identified (**Figure 5**A): i) a *C. capillata* cluster, containing most of the sequenced specimens and all sequences with the same species identity mined from GenBank (Cluster 1); ii) a cluster depicting a sister species to *C. capillata* (Cluster 2); and iii) a cluster more divergent from *C. capillata* (Cluster 3). Based on the pairwise genetic distances between the different clusters and *C. lamarckii*, ranging from 6.4 to 18.2 % (**Table 2**), the latter appeared genetically closer to *C. lamarckii*.

Since the two *C. capillata* clusters observed from the NJ-tree (Cluster 2, Cluster 3, **Figure 5**A) were divergent from *C. capillata* Cluster 1, which included most *C. capillata* sequences from GenBank, they were excluded from the subsequent diversity analyses, haplotype network, the AMOVA, and the pairwise *D* comparisons.

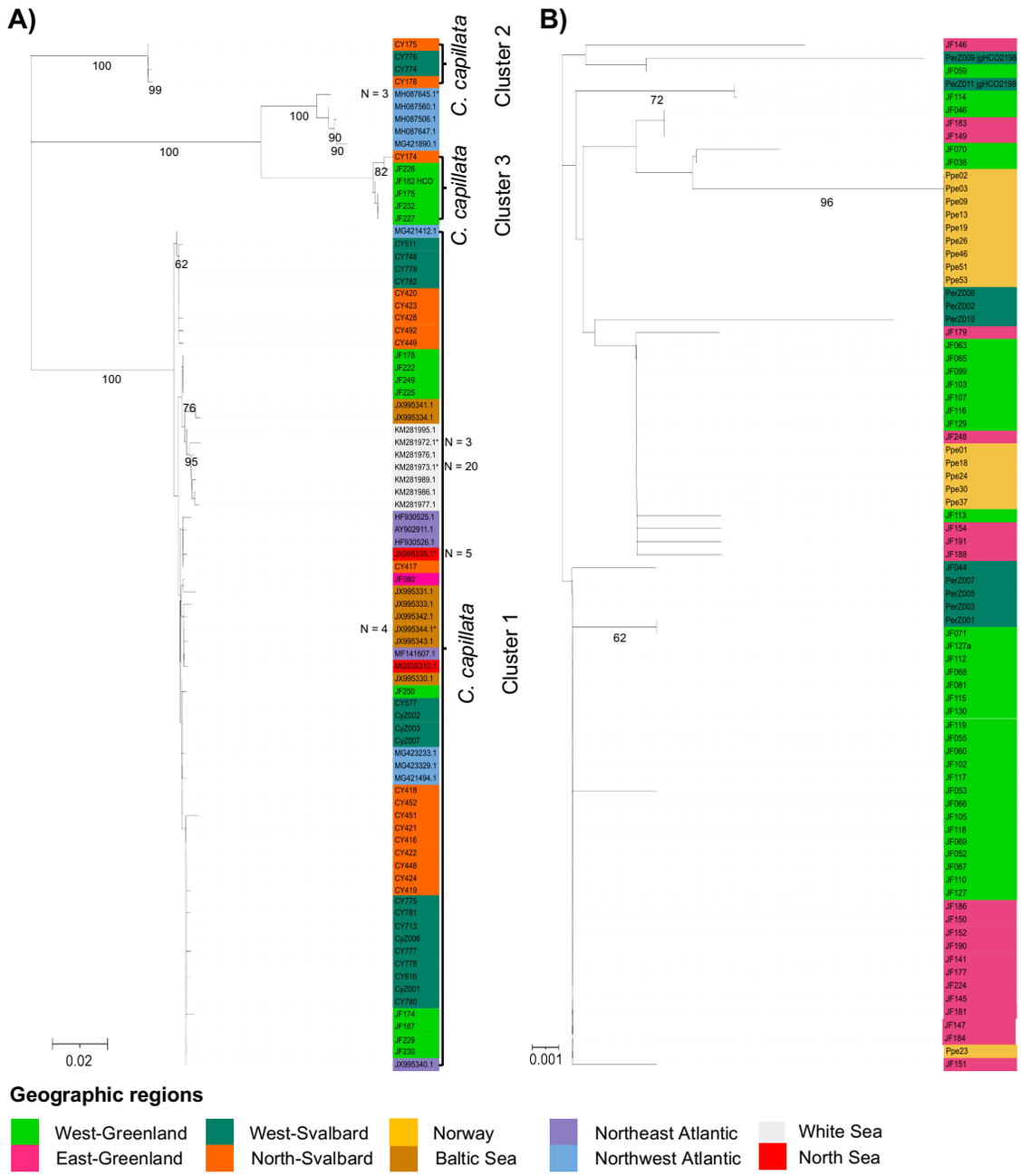


Figure 5 Neighbour-joining tree based on COI sequences of (A) *Cyanea capillata* (Total N = 113; GenBank N = 61; Study N = 52) and (B) *Periphylla periphylla* (N = 70). Tree is based on pairwise distances with bootstrap support (N reps = 2000) and is drawn to scale, with branch lengths in the same units as the evolutionary distances used to infer the tree. Evolutionary distances were computed using the Kimura 2-parameter method. Bootstrap support lower than 60 % is not reported. All ambiguous positions were removed for each sequence pair (pairwise deletion). Colours indicate geographic sampling regions. All sequences from the Baltic Sea, Northeast Atlantic, Northwest Atlantic, and White Sea were mined from GenBank (**Appendix 3**). (*) behind sample name indicates multiple identical sequences, number of sequences included is indicated by N = x behind or in front of sample name.

Table 2 Pairwise genetic distances (Kimura 2-parameter method) for the genus *Cyanea* based on mitochondrial COI. *C. capillata* Clusters 1 – 3 correspond to the clusters retrieved from the NJ tree (**Figure 5**A). *C. lamarckii* sequences were mined from GenBank (**Appendix 4**).

	C. capillata Cluster 1	*C. capillata* Cluster 2	*C. capillata* Cluster 3	*C. lamarckii*
C. capillata Cluster 1	0,0058			
C. capillata Cluster 2	0,0992	0,0015		
C. capillata Cluster 3	0,1821	0,1557	0,0042	
C. lamarckii	0,1622	0,1516	0,0643	0,0014

The average intraspecific variation (K2P distance) was 0.58 % in the *C. capillata* (Cluster 1) sequences and 0.82 % in the *P. periphylla* sequences obtained from our study. For *P. periphylla* a total of 18 polymorphic sites, 6 parsimony informative sites and 17 unique haplotypes (H) were identified among 79 specimens. Genetic diversity was described with a haplotype diversity (H_d) of 0.613 (*SD* = 0.061); nucleotide diversity (π) of 0.00501 (*SD* = 0.00068); and average number of nucleotide differences (*K*) of 1.352 (**Table 3**). In contrast, 128 polymorphic sites, 123 parsimony informative sites and 23 unique haplotypes (H) were identified for the 42 *C. capillata* (Cluster 1) specimens obtained from our study. Genetic diversity of *C. capillata* (Cluster 1) was described with a haplotype diversity (H_d) of 0.858 (*SD* = 0.041); nucleotide diversity (π) of 0.00388 (*SD* = 0.0004); and average number of nucleotide differences (*K*) of 2.556 (**Table 3**).

Table 3. Genetic diversity indices for the complete COI gene sequence data sets for *C. capillata* and *P. periphylla.* SD = Standard Deviation.

	C. capillata (all)	*C. capillata* (Cluster 1)	*P. periphylla*
Diversity indices			
Sample size (*N*)	52	42	79
Number of haplotypes (H)	23	17	17
Polymorphic sites (S)	128	20	18
Parsimony informative sites	123	5	6
Haplotype diversity (H_d ± SD)	0.901 ± 0.029	0.858 ± 0.041	0.613 ± 0.061
Nucleotide diversity (π ± SD)	0.04692 ± 0.01049	0.00388 ± 0.0004	0.00501 ± 0.00068
Average number of nucleotide differences (K)	30.078	2.556	1.352

TCS haplotype networks based on COI illustrate the diversity of the two species (**Figure 6**). One main haplotype dominates the haplotype network of *P. periphylla,* with many singletons (sequence occurring in only one individual) surrounding it. One other haplotype contains more

than 10 individuals and is most divergent from the main haplotype. There is however no clear separation according to geographic region. *C. capillata* (Cluster 1) exhibits three divergent main haplotypes, which are characterized by 10 or fewer individuals, and surrounded only by few singletons. For *C. capillata* there is no clear separation according to geographic region.

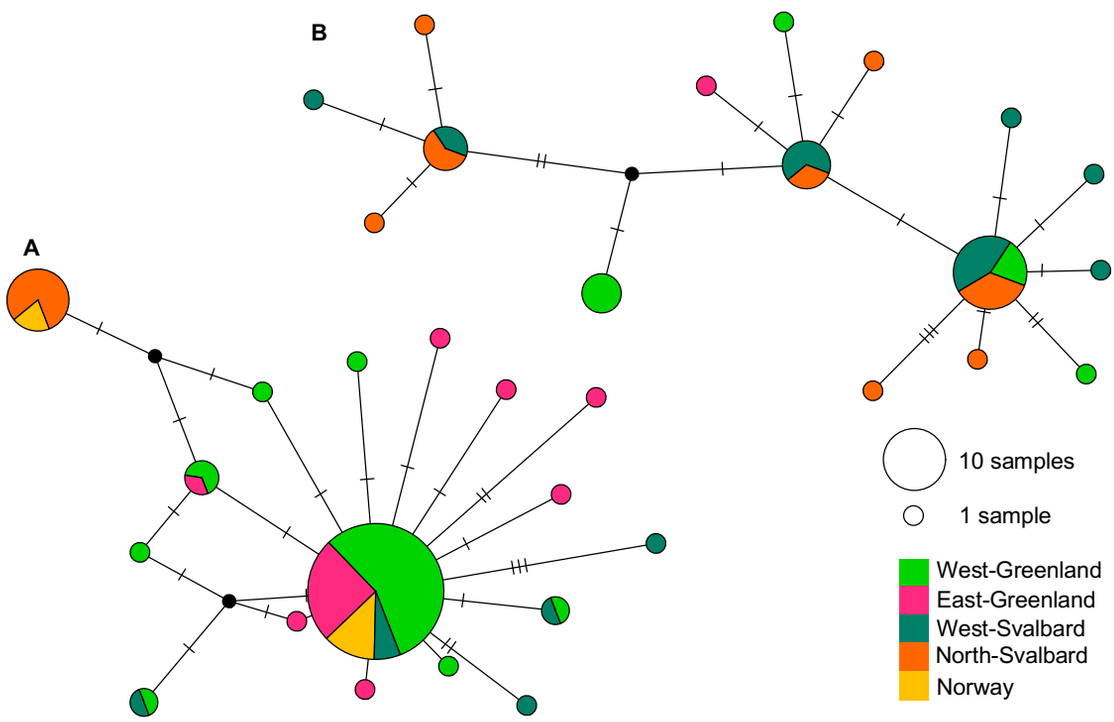


Figure 6 TCS haplotype networks for (A) *Periphylla periphylla* and (B) *Cyanea capillata* based on COI sequences. Each haplotype is represented by a circle and is coloured according to its geographic region. Circle size is proportionate to haplotype frequency, hypothetical haplotypes are represented by notches and mutations are represented by bars. The haplotype network of *C. capillata* does not include the *C. capillata* Clusters 2 & 3 that were recovered in the DNA barcoding, which were divergent from *C. capillata* Cluster 1. *C. capillata* Cluster 1 included *C. capillata* sequences from other studies and mined from GenBank as well (**Appendix 3**).

The AMOVA analysis of spatial patterns of genetic variation within and among sampled populations (**Table 4**) statistically describes the genetic structure illustrated in the haplotype networks. The variance components were low for both species at all sources (between regions, stations and in total). *P. periphylla* lacked a genetic structure with variance components of 9.5404e-06 between regions and 2.5843e-06 between stations. *C. capillata* showed a between regions variance of 3.7379e-04 and between stations variance of 1.4593e-03.

Table 4 Results of the spatial population genetic structure using the Analysis of Molecular Variance (AMOVA) based on COI. Significance tests based on 10100 permutations. Abbreviations: df = degrees of freedom, SSD = Sum of Squared Deviations, MSD = Mean Squared Deviations. α = $P \leq 0.05$.

Cyanea capillata (Cluster 1)						
Source of variation	**df**	**SSD**	**MSD**	**Variance component**	***P*-value**	**Φ-statistics**
Between regions	2	2.6313e-03	1.3157e-03	3.9540e-05	0.0747	0.04858
Between stations	17	0.01645	9.6741e-04	1.3098e-04	0.3138	0.16097
Total	41	0.03283	8.0075e-04	-	-	-
Periphylla periphylla						
Source of variation	**df**	**SSD**	**MSD**	**Variance component**	***P*-value**	**Φ-statistics**
Between regions	3	5.7866e-04	1.9289e-04	9.5404e-06	0	0.32980
Between stations	21	6.8377e-04	3.2561e-05	2.5843e-06	0.1743	0.09845
Total	78	2.0327e-03	2.6061e-05	-	-	-

Pairwise *D* comparisons reveal the genetic differentiation of the two species between the major geographic sampling regions. *C. capillata* (Cluster 1) exhibits *D* values of 0.52208 between West Greenland and West Svalbard and 0.48198 between West Greenland and North Svalbard. Between populations from Svalbard (North and West Svalbard) the *D* value is only 0.00367. *P. periphylla* shows high *D* values between West Greenland and Norway populations (*D* = 0.73386) and East Greenland and Norway populations (*D* = 0.86141). Between populations from Greenland (West and East Greenland) the *D* value is only 0.03904.

Table 5 Results of pairwise *D* values (actual differentiation after Jost, 2008) based on COI for genetic connectivity between major geographic regions.

Cyanea capillata (Cluster 1)				
	North Svalbard	**West Svalbard**	**West Greenland**	
North Svalbard	0			
West Svalbard	0.00367	0		
West Greenland	0.48198	0.52208	0	
Periphylla periphylla				
	West Greenland	**East Greenland**	**Norway**	**Svalbard**
West Greenland	0			
East Greenland	0.03904	0		
Norway	0.73386	0.86141	0	
Svalbard	0.25553	0.23387	0.50166	0

3.2 Scyphozoan diversity in Arctic fjords

The metabarcoding of sediment eDNA from 10 stations around Svalbard revealed 2258 OTUs. A total of 41 phyla, 81 classes, 176 orders, 214 families, 249 genera, and 264 species were assigned (**Figure 7**). Most abundant phyla were Annelida (39.8 % RRA), Bacillariophyta (29.2 % RRA) and Dinoflagellata (12.3 % RRA) (**Appendix 5**). Cnidaria represented 0.2 % of the relative reads. DNA of *P. periphylla* was not detected at any station. *C. capillata* was detected at six out of ten stations (stations 02, 06, 10, 13, 15, 23).

At all stations where *C. capillata* was caught with nets or trawls, eDNA of this species was found, except for station 21, where no eDNA was detected in the metabarcoding dataset. At stations 06 and 13, only eDNA was found, but no *C. capillata* specimens were recovered with the net or trawl hauls (**Table 6**). The zooplankton species composition revealed with plankton net hauls and trawls differed in many ways from the pelagic community composition revealed with sediment eDNA (**Table 6**). Several GZP species that were collected in nets (*Beroe* spp*., Aglantha digitale, Euphysa flammea, Halitholus cirratus*) were not found in the DNA dataset. Similarly, also crustacean zooplankton species that were caught with nets were not well represented in the eDNA (e.g., *Themisto* spp., *Thyssanoessa* spp.). For the nekton, out of the 10 fish families recovered in the eDNA dataset, only two fish families were recovered by the nets and trawls. The family of the Gadidae, which could represent polar cod and/or Atlantic cod, was more frequently detected with eDNA (nine out of ten stations) compared to net and trawl sampling (two out of ten stations).

In **Figure 8** the RRAs of the pelagic metazoan community recovered in sediment eDNA are shown. Most of the stations are dominated by Arthropoda, with read percentages of 50 or more. Cnidaria are well represented at station 01 and 10 with about 20 % of the reads, and even dominate the pelagic DNA at stations 02, 06, and 24 (RRAs > 50 %).

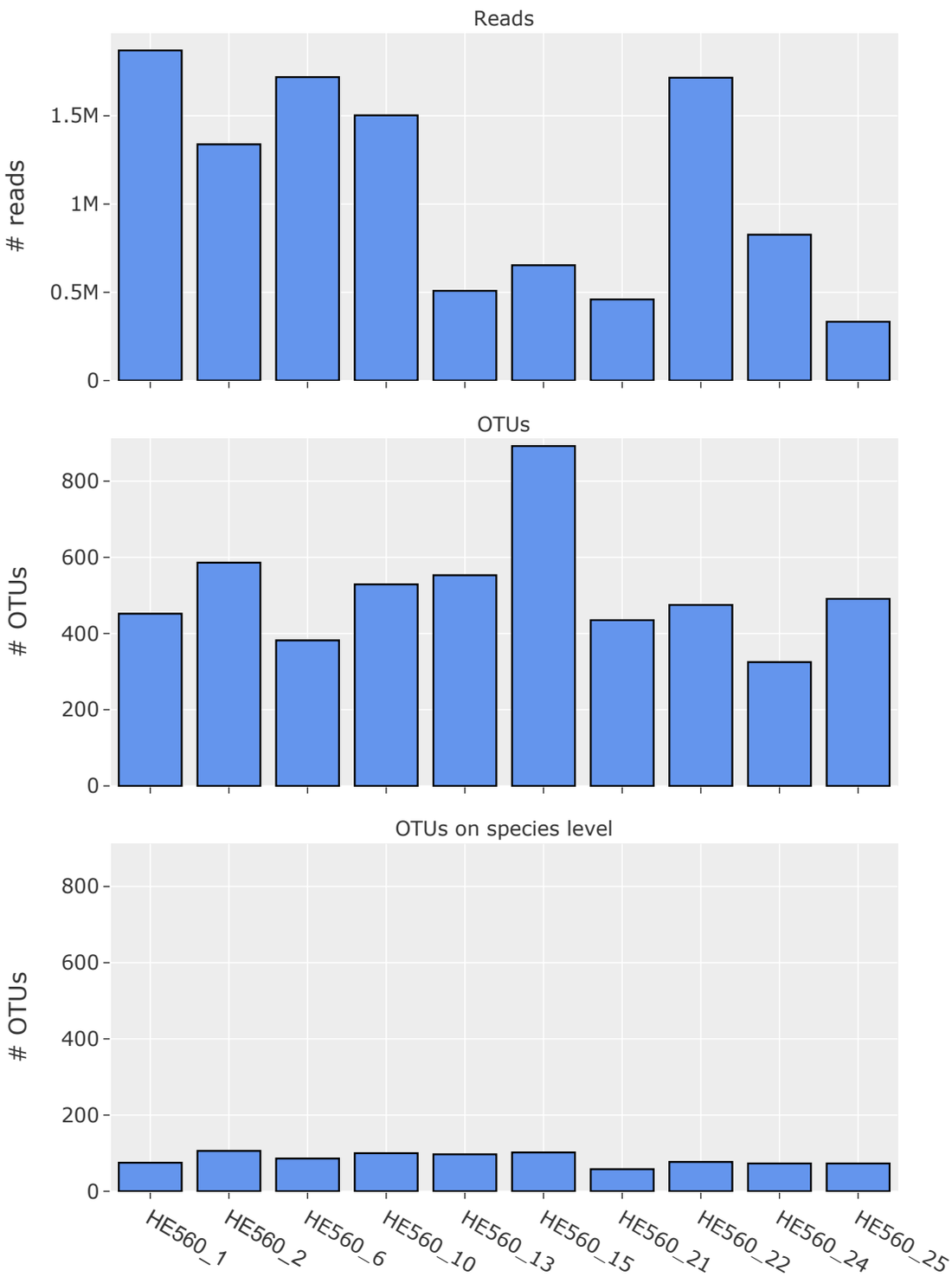
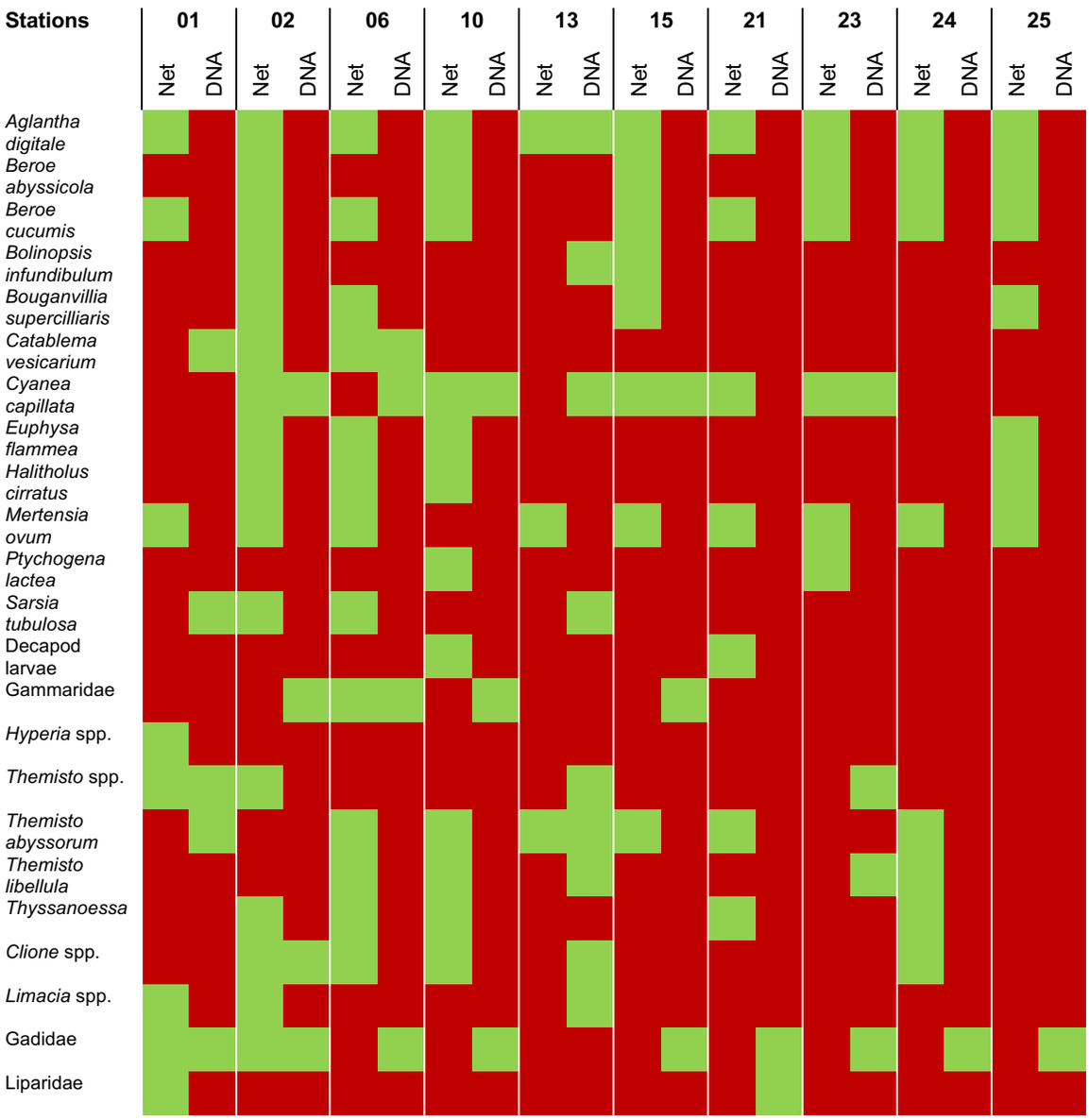


Figure 7 Basic statistics of the eDNA sediment dataset, containing samples from 10 stations around Svalbard. Shown are (from top to bottom) the number of reads per station, the number of OTUs per station and the number of OTUs assigned on species level per station.

Table 6 Comparison of zooplankton and nekton (= fish) species in net or trawl catches (Net) or in sediment eDNA (DNA) from 10 stations at HE 560 (Stations: 01, 02, 06, 10, 13, 15, 21, 23, 24, 25). Shown is only detection (green) or no detection (red) of the species at each station.



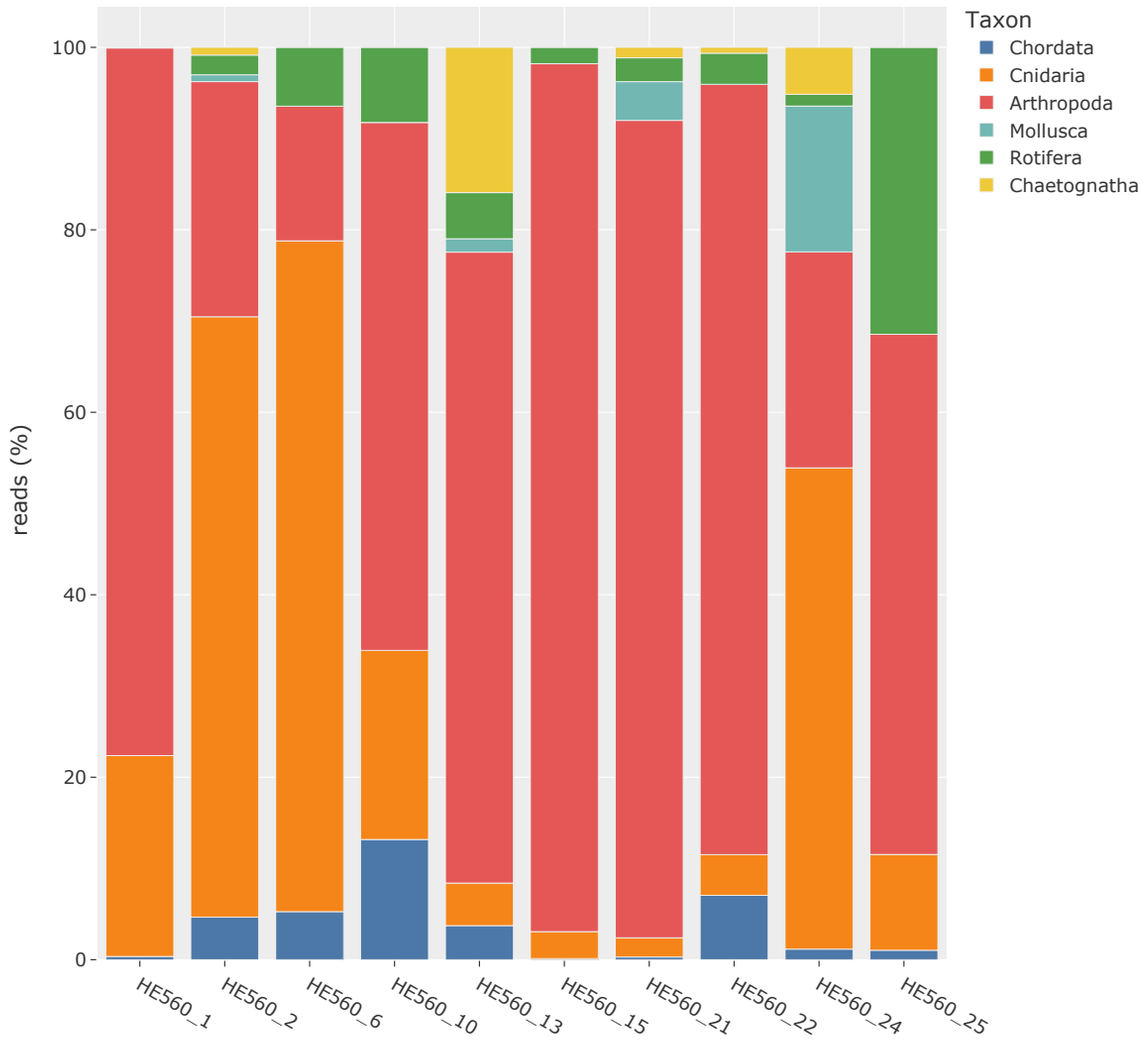


Figure 8 Relative read abundances of the pelagic metazoan community at 10 stations around Svalbard, collected from the oceanographic cruise HE 560. Shown are the pooled reads of the PCR replicates of each station. Only metazoan and pelagic organisms were considered.

A nMDS model was produced (**Figure 9**) to illustrate the difference in community structure between the Arctic-influenced North Svalbard fjords and the Atlantic-influenced West Svalbard fjords. The nMDS plot shows that samples from North Svalbard cluster together and are separated from the cluster of samples originating from West Svalbard. The samples from the North Svalbard fjords showed a higher variance between each other and are more widely spread than the samples from West Svalbard.

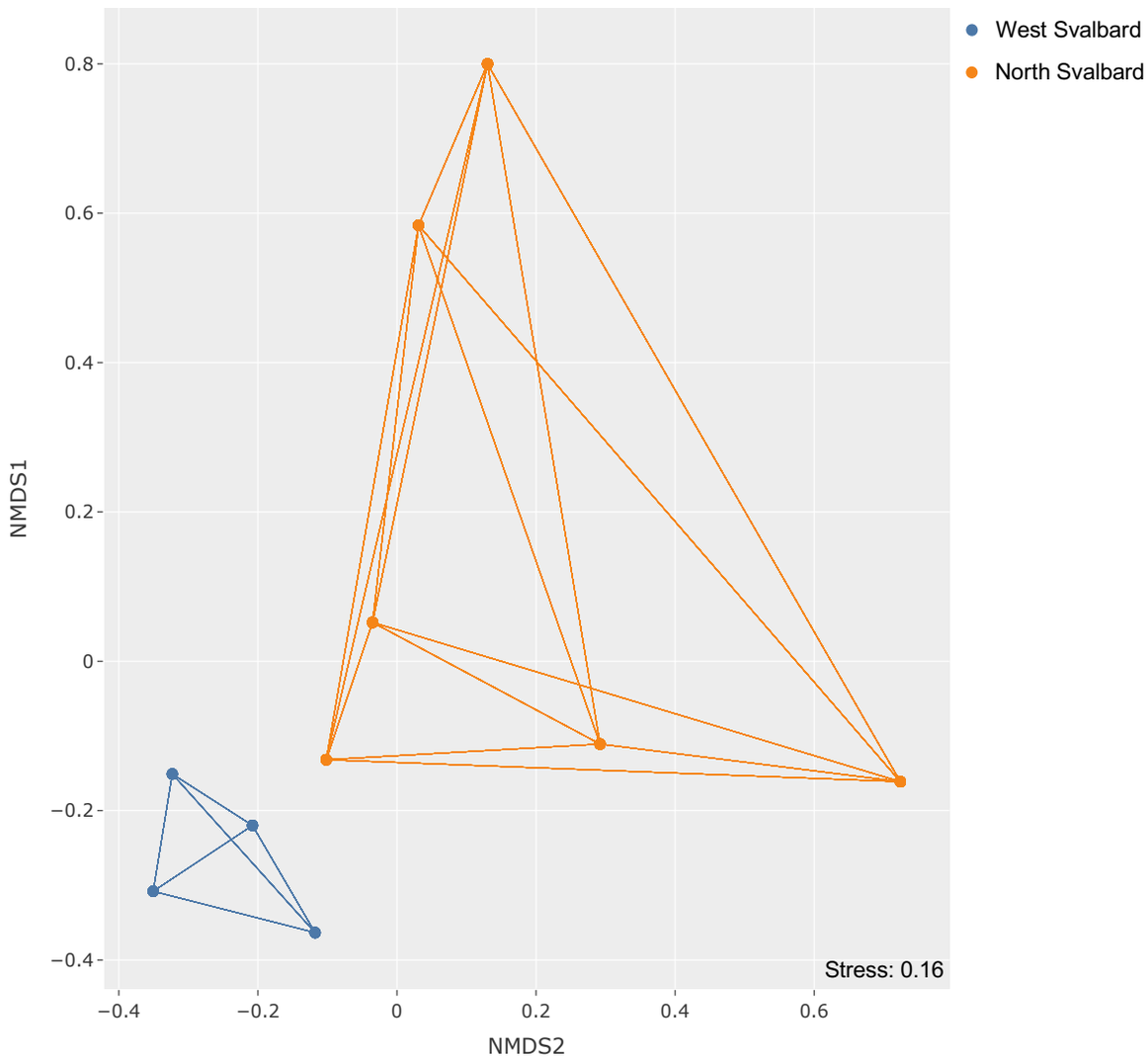


Figure 9 nMDS plot for sediment eDNA samples around Svalbard. Colours show the two major geographic regions: the Arctic-influenced North Svalbard fjords, and the Atlantic-influenced West Svalbard fjords. The model shows 2 dimensions (*k*) with a raw stress of 0.16.

The differences between North and West Svalbard pelagic communities were also compared on phylum level and are illustrated in **Figure 10**, whilst also comparing them to the species richness revealed with the net catches at the same stations. For most phyla, a noticeable difference between north and west is visible. Cnidaria for example show higher numbers of species in the North Svalbard fjords than in the West Svalbard fjords. This difference is reflected in both eDNA (6 – 8 species in North Svalbard, 3 – 7 species in West Svalbard) and in net catches (1 – 7 species in North Svalbard, 1 – 4 species in West Svalbard). The actual species recovered by both methods were often different (see **Table 6**) as well. Additionally, different phyla were detected by both methods. For example, Chaetognatha and Rotifera were not recovered by the net catches, because they were not looked for during sorting. In contrast, Ctenophora were not detected using metabarcoding likely due to primer biases. It is however important to note, that an absence from the dataset does not mean an absence from the ecosystem, since both sampling methods only show a snapshot, and inherent biases exist with regard for both methods. Effects of these inherent biases can be seen in **Figure 10**, where Mollusca (= pteropods) and Chordata (= fish) are only present in North Svalbard. At the later stage of the cruise, which coincides to the West Svalbard stations, they were no longer sorted out.

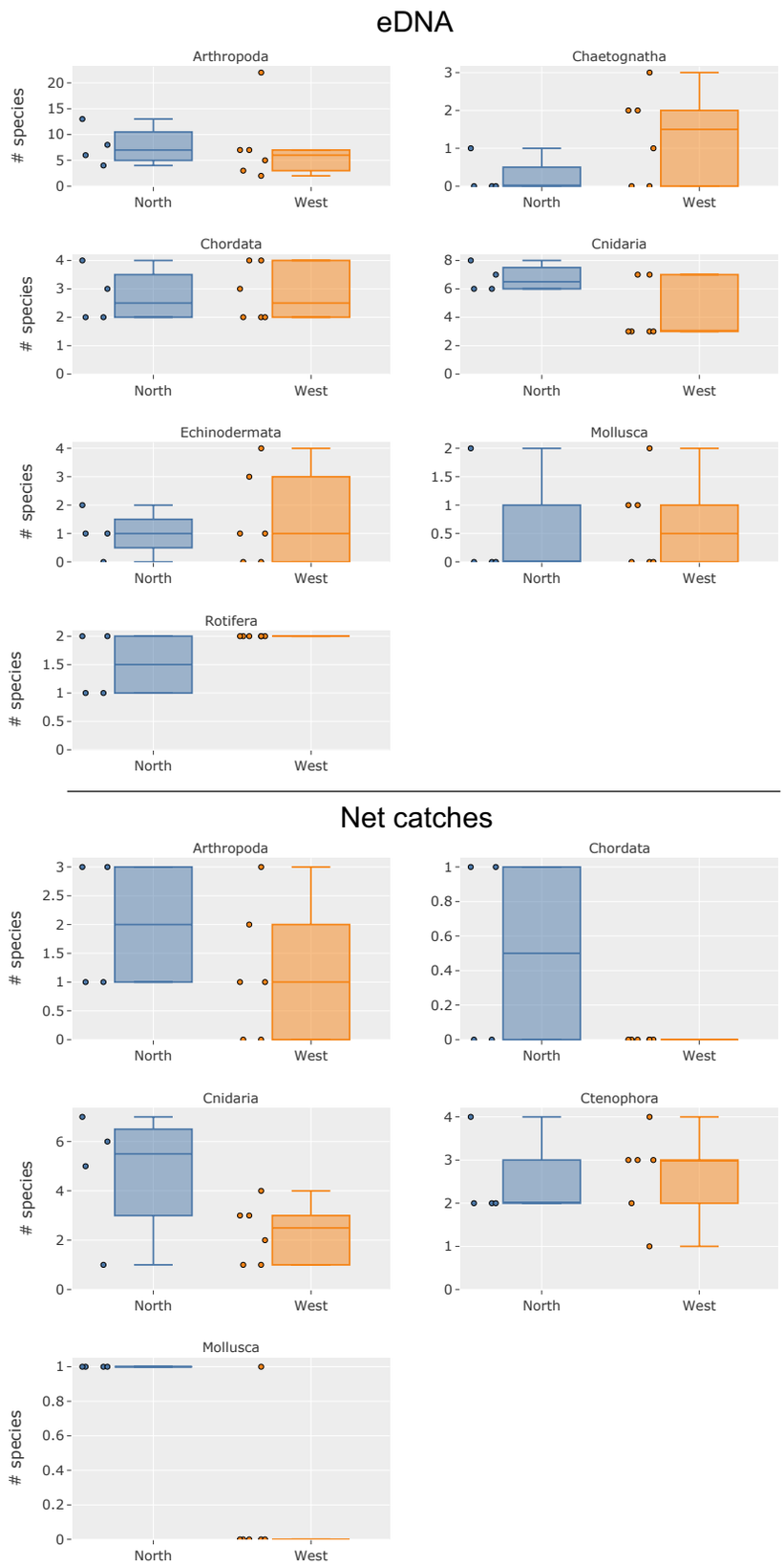


Figure 10 Comparison of eDNA (top) and net catches (bottom), showing the number of species per phylum between North Svalbard (blue) and West Svalbard (orange) fjords.

3.3 Species-specific detection of scyphozoans

The length of the designed species-specific primers varied from 20 bp to 24 bp, the lengths of the COI regions amplified by them between 76 bp and 142 bp. The sequences for all designed primers are shown in **Table 7**.

Table 7 Sequences of all primer pairs designed for *C. capillata* (Cyacap) and *P. periphylla* (Periperi) located on the COI gene region. Suffix "_F" = forward primer, suffix "_R" = reverse primer.

C. capillata		***P. periphylla***	
Cyacap_1_F	5'-GGTGCTTCCTCTATAATGGG-3'	Periperi_1_F	5'-TTAGCYAGYATTCAAGCACA-3'
Cyacap_1_R	5'-AATGGCTGTTACCAGKACTG-3'	Periperi_1_R	5'-CCATRGTYAAACCTGGTGCR-3'
Cyacap_2_F	5'-TTAGCYGGGGCAATTACAAT-3'	Periperi_2_F	5'-GCACCAGGTTTRACYATGGA-3'
Cyacap_2_R	5'-GGTGTTGRAACAAGATKGGG-3'	Periperi_2_R	5'-CCRGCYAATACTGGTATRGC-3'
Cyacap_3_R	5'-GGTTGGACTATTTATCCTCCTCT-3'	Periperi_3_R	5'-TCAAGCACATTCAGGAGGRG-3'
Cyacap_3_R	5'-TGGCTCCCATTATAGAGGAAG-3'	Periperi_3_R	5'-VGCCATAATAGAACTAGCYCCY-3'
Cyacap_4_F	5'-TTCCTCTATAATGGGAGCCA-3'	Periperi_4_F	5'-TTAGCTAGCATTCAAGCACA-3'
Cyacap_4_R	5'-AATGGCTGTTACCAGTACTG-3'	Periperi_4_R	5'-TCCATAGTTAAACCTGGTGC-3'
Cyacap_5_F	5'-TTAGCTGGGGCAATTACAAT-3'	Periperi_5_F	5'-TAGCTAGCATTCAAGCACAT-3'
Cyacap_5_R	5'-AAACAAGATTGGGTCTCCTC-3'	Periperi_5_R	5'-CCATAGTTAAACCTGGTGCT-3'
Cyacap_6_F	5'-TTAGCTGGGGCAATTACAAT-3'	Periperi_6_F	5'-AGCACCAGGTTTAACTATGG-3'
Cyacap_6_R	5'-GAAACAAGATTGGGTCTCCT-3'	Periperi_6_R	5'-CCGGCTAATACTGGTATAGC-3'
Cyacap_7_F	5'-GGAACAGGTTGGACTATTTATCC-3'	Periperi_7_F	5'-TTCAAGCACATTCAGGAGGA-3'
Cyacap_7_R	5'-TGGCTCCCATTATAGAGGAAG-3'	Periperi_7_R	5'-GGCCATAATAGAACTAGCTCCT-3'
Cyacap_8_F	5'-GAACAGGTTGGACTATTTATCCTC-3'	Periperi_8_F	5'-GCATTCAAGCACATTCAGGA-3'
Cyacap_8_R	5'-TGGCTCCCATTATAGAGGAAG-3'	Periperi_8_R	5'-GGCCATAATAGAACTAGCTCCT-3'

For each primer, T_M ranged between 54.8 and 57.2 °C. GC-content was between 40 and 50 %. Out of the eight initially designed primer pairs for each species (**Table 7**) the three with the least probability to from self-dimers and cross-amplify with other species were selected after in-silico testing and ordered for *in-vitro* and *in-situ* testing (Cyacap_1, Cyacap_2, Cyacap_3; Periperi_1, Periperi_2, Periperi_3). Properties of those primers are described in **Table 8**.

Table 8 Properties of the 3 primer pairs used in *in-vitro* testing for each species (*C. capillata* = Cyacap; *P. periphylla* = Periperi; suffix _F = forward primer, suffix _R = reverse primer). Shown are GC-content in percentages, melting temperature T_M in °C and the length of the COI region amplified by the primer pairs (Amplicon length) in bp.

	GC-content [%]	T_M [°C]	Amplicon length [bp]
Cyacap_1_F	50.0	55.0	120
Cyacap_1_R	45.0	55.1	
Cyacap_2_F	40.0	55.0	97
Cyacap_2_R	45.0	55.1	
Cyacap_3_F	43.5	56.8	112
Cyacap_3_R	47.6	56.3	
Periperi_1_F	40.0	55.1	142
Periperi_1_R	45.0	55.0	
Periperi_2_F	45.0	55.0	95
Periperi_2_R	50.0	54.9	
Periperi_3_F	50.0	57.2	76
Periperi_3_R	45.5	56.8	

Figure 11 shows the process of *in-vitro* and *in-situ* testing. The first *in-vitro* test PCR revealed that one primer pair per species (Cyacap_2 and Periperi_2) amplified the target DNA well, showing one band in the electrophoresis gel at the respective amplicon target length (**Appendix 7**A). Additional testing with DNA extract of other scyphozoan jellyfish species (*Atolla* spp., *Cyanea lamarckii*) revealed specificity for only the primer pair Cyacap_2, which amplified solely the target DNA of *C. capillata* (Cluster 1 well, Clusters 2 & 3 sparsely) (**Appendix 7**B, C). Periperi_2 additionally amplified DNA extract of *Atolla* spp. and was thus excluded from further testing. The *in-situ* testing using DNA extract from the eDNA mesocosm experiment (**Figure 4**) resulted in the amplification of the target sequence in all samples where *C. capillata* was present, and no amplification of experimental (mesocosm without added jellyfish tissue) and negative controls (PCR mix without added DNA extract) (**Appendix 7**D).

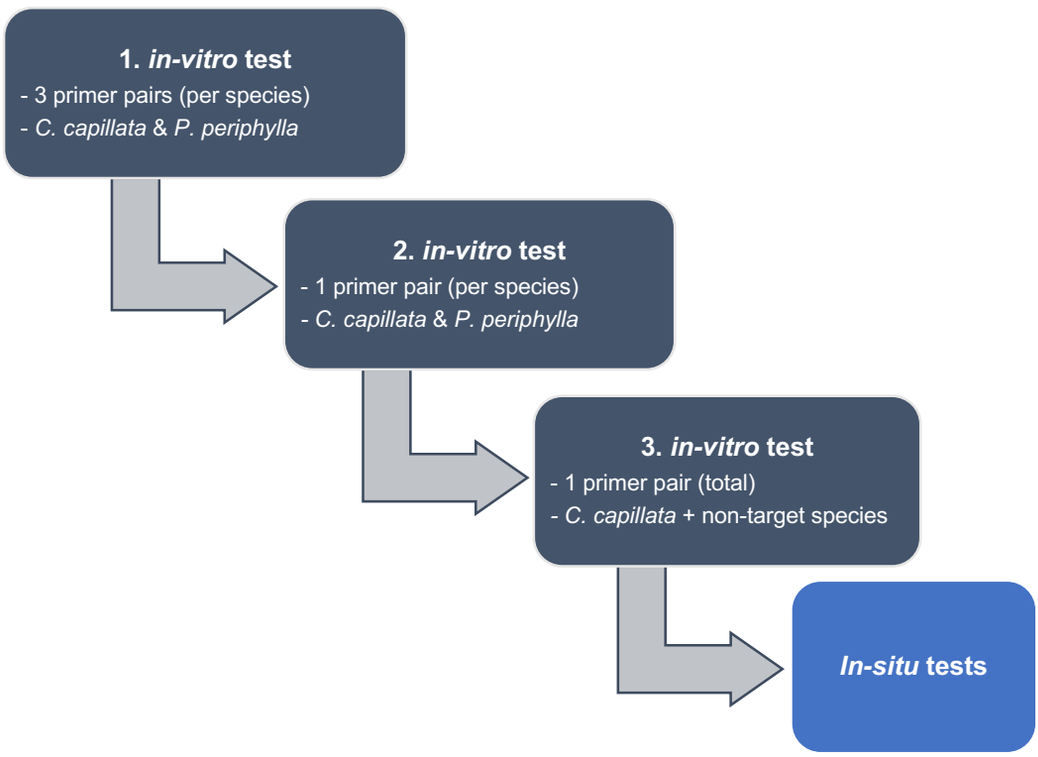
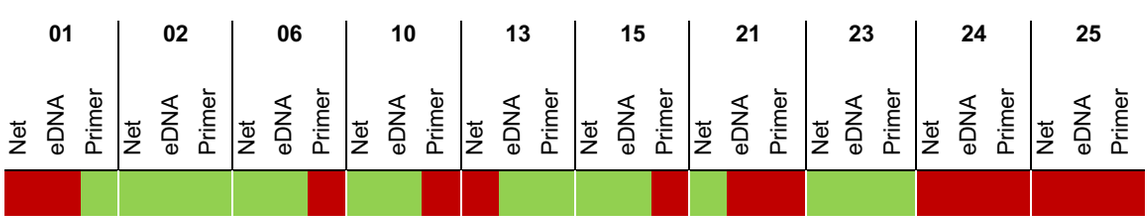


Figure 11 Schematic overview of the primer testing process. From the initial test with all designed primers for both species (*C. capillata* & *P. periphylla*) to the *in-situ* tests only containing 1 primer pair for *C. capillata*.

In the last primer-test, Cyacap_2 was applied on the DNA extractions of sediment samples from Svalbard (HE 560 cruise) in a PCR. Out of the eleven samples where *C. capillata* reads were detected using metabarcoding, six samples (2_2b, 6_1c, 15_2a, 22_1b, 22_2b, 22_2c) showed clearly visible bands in the electrophoresis gel (**Appendix 7**E). Two samples showed very weak bands (6_1a, 15_3c) and three samples showed no amplification of the target sequence (10_1b,10_2c, 15_3a). Additionally, amplification was also successful for other samples, where the metabarcoding did not identify *C. capillata*. A comparison between the three detection methods of net or trawl catches, eDNA metabarcoding, and species-specific primers in a PCR at the ten sampled stations are illustrated in **Table 9**.

Table 9 Comparison of *C. capillata* detection with different methods: net or trawl catches (Net), eDNA metabarcoding (eDNA), and species-specific primers in a PCR (Primer). Shown is only detection (green) or no detection (red) of *C. capillata* at each station (01, 02, 06, 10, 13, 15, 21, 23, 24, 25).



4 Discussion

4.1 Genetic connectivity of scyphozoan populations

The two large scyphozoan jellyfish species *P. periphylla* and *C. capillata* were analysed for genetic diversity, genetic structure and connectivity in Svalbard, Greenland, and a Norwegian fjord (*P. periphylla*), using the mitochondrial COI region. Overall, moderate (*P. periphylla*) to high (*C. capillata*) levels of diversity and lack of genetic structure in both species could be observed. Species-level lineages with three divergent clusters were uncovered for *C. capillata*. One cluster (*C. capillata* Cluster 1) can be assumed to be *C. capillata* sensu stricto, as it includes most sequences from our study as well as most sequences mined from GenBank and classified as *C. capillata*, except for one cluster of sequences comprising samples from the Northwest Atlantic. Both other clusters (*C. capillata* Clusters 2 & 3) show K2P distances higher than 9 % compared to Cluster 1 and can therefore be classified as species-level lineages, divergent from *C. capillata* sensu stricto. Cluster 3, which is most divergent from *C. capillata* sensu stricto (Cluster 1), consists of almost exclusively specimens from West Greenland, with only one exception from North Svalbard. The cluster is also closely related to another cluster divergent from *C. capillata* sensu stricto, which consists of sequences mined from GenBank of specimen sampled from the Northwest Atlantic (North American coast). Additionally, Cluster 3 is more closely related to *C. lamarckii*, the sister species of *C. capillata*, than the other clusters uncovered in our study. The second cluster we found in our analysis (*C. capillata* Cluster 2) consists solely of specimens from the Arctic (North & West Svalbard).

P. periphylla noticeably lacks a genetic structure according to its geography and its haplotypes are geographically homogenously distributed. This may imply ongoing or recent genetic exchange between populations even across large distances, from South Greenland to Svalbard. Similar findings have been reported by Abboud *et al.* (2018) who found the least genetic differentiation in *Periphylla* compared to 15 other genera of jellyfish and even across distances of 1000s of kilometres. They stated the importance of the sessile polyp stage of many jellyfish in promoting higher genetic structure. Since *Periphylla* is holoplanktonic, which means it is missing a sessile polyp stage (Youngbluth & Båmstedt, 2001), it has a wider species range and increased population connectivity and gene flow compared to meroplanktonic scyphozoans. *Pelagia noctiluca* is another holoplanktonic scyphozoan jellyfish and also lacks genetically or geographically distinct populations in its distribution across the Mediterranean Sea and East Atlantic, despite two clusters being identified (Stopar *et al.*, 2010). Despite the visible lack of geographic structuring revealed by the haplotype network and AMOVA analysis, pairwise *D* values unveil that *P. periphylla* populations of different geographic regions are genetically differentiated. The high *D* values between Greenland and

Norway populations indicate that despite the apparent high population connectivity, hydrogeographic barriers still exist. In the future, this could potentially cause genetic separation and lead to patterns similar to the multiple species-level lineages we uncovered for *C. capillata*.

P. periphylla exhibited moderate diversity on the COI region with a haplotype diversity value of 0.613 (± 0.061). This contrasts with other analyses of scyphozoan diversity using COI, and with the results of *C. capillata*. Mitochondrial diversity of scyphozoan jellyfish has often been described as high, exceeding H_d of 0.9 and reaching up to $H_d = 1$ (Dawson, 2005a; Edelist *et al.*, 2022; Ras *et al.*, 2020; Stopar *et al.*, 2010). Descriptions of lower haplotype diversity in scyphozoan jellyfish is rare but was found for example for *Chrysaora hysoscella* from the Benguela upwelling system, with a comparable H_d value of 0.67 (Ras *et al.*, 2020). The holoplanktonic nature of *P. periphylla*, which increases the probability of a high population connectivity, is likely responsible for its lower genetic diversity. High population connectivity and consequently high gene flow as a result of effective dispersal moves alleles between populations, making them genetically more similar and thus decreasing genetic diversity and structure. Additionally, it is important to note that we analysed a shorter COI fragment in *P. periphylla* (313 bp) than in *C. capillata* (658 bp), which affects the haplotype diversity and makes comparisons between the two species difficult. The smaller fragment length decreases the probability of finding base pair differences, thus potentially reducing haplotype diversity. To compare the two target species of our study, the same part of the COI gene would need to be investigated, e.g., the 313 bp Leray-fragment, which lies within the 658 bp Folmer-fragment or better yet the whole Folmer-fragment in both species.

P. periphylla's ecology and distribution patterns could greatly influence its genetic diversity and connectivity and have a broad impact on a possible future range expansion. Being a holoplanktonic species and passive drifter helps in easily and widely connecting populations. Thus, it has been described as a cosmopolitan species (Geoffroy *et al.*, 2018; Youngbluth & Båmstedt, 2001). These characteristics are well mirrored by our phylogeography results. Since *P. periphylla* is not well characterized genetically on a global scale it cannot be ruled out, that a higher genetic structure or even several lineages of the species exist when global populations are considered. Even though cosmopolitan species are often assumed in marine plankton due to the high dispersal potential, many molecular studies now cast doubt on this. Over the past decades, cryptic species have been discovered for many jellyfish genera, like *Cyanea*, *Aurelia*, *Phacellophora*, and *Physalia* (Dawson, 2005b; Lawley *et al.*, 2021; Moura *et al.*, 2022; Pontin & Cruickshank, 2012). Other zooplankton species supposed to be cosmopolitan, like the copepod *Oithona similis*, have also been found to consist of several mitochondrial lineages (Cornils *et al.*, 2017).

Using only COI as genetic marker, limits the ability to make assertions about present day gene flow. As a marker suitable for assessing inter- and intraspecific genetic diversity, the mitochondrial COI gene is less suitable to infer recent gene flow and selection. To infer future changes in the distribution of *P. periphylla* under changed climatic conditions, it is important to know the genetic composition of the species. Therefore, more research needs to be done to uncover its diversity to greater detail, by incorporating multiple genetic markers into the analyses and using more samples. To understand present gene flow dynamics and adaptation potential through selection, microsatellites or SNPs (single nucleotide polymorphisms) would need to be investigated, especially in view of ongoing and future range shifts.

Cyanea *capillata* sensu stricto shows a lack of geographic structure, similar to *P. periphylla*, which is in line with other studies on scyphozoan phylogeography (Abboud *et al.*, 2018; Edelist *et al.*, 2022; Ras *et al.*, 2020; Stopar *et al.*, 2010). This has repeatedly been explained by their high dispersal potential due to their planktonic stages and the lack of geographic barriers in their marine habitats. On the other hand, *C. capillata* sensu stricto shows a high intraspecific diversity with a haplotype diversity value of 0.901 (± 0.029). Being a meroplanktonic species, *C. capillata* has smaller species boundaries than its holoplanktonic counterpart *P. periphylla*. The sessile benthic polyp stage, which reproduces asexually, has an important role in promoting local population persistence (Abboud *et al.*, 2018), since its distribution is limited to the shore, where suitable rocky substrate can be found (Brewer, 1976, 1984; Holst & Jarms, 2007). Therefore, the genetic mixing is partially mitigated, which fosters diversity, as alleles are less easily moved between populations.

Three species-level lineages were found of what was thought to be one species – *C. capillata*. The species composition of the genus *Cyanea* has been subject of debate for many decades and undergone many revisions (Brewer, 1991; Dawson, 2005b; Haeckel, 1880; Kramp, 1961; Russell, 1970). *Cyanea* species have been synonymized and rebutted again several times (Dawson, 2005b; Kramp, 1961; Russell, 1970). Especially the state of North Atlantic *Cyanea* is yet to be resolved, as some studies indicate higher species richness than previously estimated (e.g., Bayha *et al.*, 2010). Most recently, Holst & Laakmann (2014) investigated eastern Atlantic *Cyanea* species morphologically and molecularly. Their study could clearly distinguish *C. capillata* and *C. lamarckii* genetically, with distances of 15 – 18.5 %. This is comparable to the K2P-distances between the *C. capillata* clusters we uncovered ranging from 9.9 to 18.2 %. What can be seen in our analysis, is that one cluster (Cluster 3) consists mainly of West Greenland/Northwest Atlantic sequences. The comparably high divergence from *C. capillata* sensu stricto (Cluster 1) suggests an older separation process. In contrast, the other cluster divergent from *C. capillata* we uncovered (Cluster 2) only consisted of Arctic specimens. The lower distances to *C. capillata* sensu stricto allude to a more recent separation

process. The apparent segregation of Arctic (Cluster 2) and Northwest Atlantic (Cluster 3) lineages from the main lineage (Cluster 1) suggests historical gene-flow disruptions caused by geographic isolation and differing hydrodynamic regimes. Between the two populations lies Greenland and the opposing major ocean currents of the Fram Strait: the south-bound East Greenland Current and the north-bound West Spitsbergen Current. This physical separation by Greenland and the Atlantic might have caused the divergence of the two lineages. The main cluster, *C. capillata* sensu stricto Cluster 1, consisted of haplotypes from all sampled geographic regions, as well as additional regions sampled by other studies (retrieved from GenBank). This indicates a high population connectivity, similar to our results for *P. periphylla.* Nevertheless, even within this cluster, higher pairwise *D* values can be found between West Greenland and Svalbard populations. This proposes a lowered genetic connectivity between the two regions, supporting the hypothesis of a separation process due to geographical distance. Findings of cryptic diversity and several species-level lineages have recently also been uncovered for the scyphozoan jellyfish *Phacellophora* from the North American Atlantic and Pacific coasts (Moura *et al.*, 2022). This separation was most likely the result of historical gene-flow disruptions through the Arctic (Moura *et al.*, 2022). Another possible origin of species-level lineages with overlapping distributions could be hybridisation of closely related *Cyanea* species in the respective regions (West Greenland; Svalbard). Hybridisation could occur between closely related species with an overlapping geographic distribution, such as *C. capillata* and *C. lamarckii* in the North Atlantic. This has also been hypothesized by Pontin & Cruickshank (2012) for *Physalia*, a siphonophore species, in New Zealand. Overall, the high population connectivity we uncovered for *C. capillata* sensu stricto in combination with the occurrence of multiple divergent lineages might have important implications for future range expansions of the species. Intraspecific genetic admixture, which describes multiple divergent genetic lineages coming into gene flow contact and interbreeding, and hybridisation of species-level lineages could help to establish the species in novel habitats (Rius & Darling, 2014).

Comparisons between the two target species of this study (*P. periphylla* and *C. capillata*) must be seen cautiously, because the size of the COI fragment used for the genetic diversity analyses differed. Additionally, the geographic regions analysed differed between both species: *P. periphylla* was sampled in West and East Greenland, Norway and one Svalbard fjord (Kongsfjorden); *C. capillata* was only sampled from West Greenland and multiple Svalbard fjords (Arctic influenced North Svalbard & Atlantic influenced West Svalbard). As a result, direct inferences will likely vary by design, as the basic parameters of the analysis do not match. Furthermore, there is no knowledge about the effective population sizes (N_e) of the two species, which would be necessary to make tangible comparisons between them. Populations with large N_e have a higher genetic variation, because more new diversity is

brought in by a high number of breeding events, and less alleles are lost to genetic drift (Charlesworth, 2009). Thus, calculations of N_e would be necessary to explain differences in genetic variation. Another factor which makes explanations of genetic diversity and structure of jellyfish difficult and sometimes even unpredictable, is their ability to form blooms. It is unknown what effects the periodic increase of populations sizes followed by a sharp decline in population sizes has on genetic diversity and N_e. Typically, it is expected that species maintaining large populations show a high diversity (Kimura, 1983), while sharp declines in population size causes the bottleneck effect and reduce diversity (Nei *et al.*, 1975). Both species have been reported to form blooms under some circumstances (Crawford, 2016; Geoffroy *et al.*, 2018; Youngbluth & Båmstedt, 2001), which means their population sizes can fluctuate drastically. For holoplanktonic species like *P. periphylla*, this could potentially cause a bottleneck effect if the entire population collapses after a bloom and no larvae are produced yet. Meroplanktonic species like *C. capillata* would keep their genetic standing stock in the shape of their polyps after a medusae population collapse. This makes it difficult to predict and explain their genetic structures and diversity, as the population history at the different locations remain unknown although it could have had a tremendous influence on the genetic variation of the respective populations.

The phylogeographic findings from this study provide a variety of implications for future range expansions of both *C. capillata* and *P. periphylla*. Conspicuous in both species is the lack of genetic structure based on geographic populations. This is an important trait when it comes to range expansions (Shirk *et al.*, 2014). Undifferentiated origin populations, i.e., populations with low genetic structure, contain much of their overall diversity within populations (Hamrick & Godt, 1996; Novak & Mack, 1993). This means that a single event can introduce the genetic diversity of the source population to a new habitat, which reduces founder effects (Hamrick & Godt, 1996; Novak & Mack, 1993) and increases the likelihood of the species' becoming established. Additionally, moderate to high intraspecific genetic diversity could be detected in both species, which might influence the possibility of successful range expansion as well. Generally, a high genetic diversity of source populations is associated with a positive success of new colonizing populations during a range expansion (Crawford & Whitney, 2010; Willi *et al.*, 2006), because stable or high diversity has evolutionary advantages in adaptations to new environments (Crawford & Whitney, 2010; Yang *et al.*, 2008). Usually, this high diversity is the result of frequent genetic exchange, as we propose for *P. periphylla* and *C. capillata*, due to their facilitated dispersal as passively drifting jellyfish. Overall, genetic diversity retains biological variation and thus ensures ecological success which makes establishment of species in new environments more likely.

4.2 Scyphozoan diversity in Arctic fjords

4.2.1 Detecting jellyfish with metabarcoding from sediment samples

P. periphylla could not be detected from the sediment eDNA samples using metabarcoding. Contrarily, *C. capillata* was detected at six sampling stations. These findings contrast our hypothesis, which assumes that both *P. periphylla* and *C. capillata* DNA could be found in different fjords around Svalbard. Based on the trend of increasing numbers of *P. periphylla* reports and catches in Svalbard, we expected to find DNA in sediments of Atlantic-influenced fjords, despite having caught no specimens with nets or trawls during the HE 560 expedition. These assumptions were made based on previous descriptions of *P. periphylla* in Svalbard fjords. Geoffroy *et al.* (2018) caught single *P. periphylla* individuals in Rijpfjorden (= station 01) and Isfjorden (close to station 22) in May 2017. They also captured multiple specimens in Kongsfjorden (not sampled for eDNA in this study) in January 2017. The species is already ubiquitous in Greenland and Norwegian seas (Dalpadado *et al.*, 1998) and could thus be easily advected into Svalbard fjords via the West Svalbard Current (WSC) (Aagaard *et al.*, 1987; Gjøsæter *et al.*, 2017; Meyer-Kaiser *et al.*, 2022). Contributing to our assumptions is that *P. periphylla* is a deep-sea species (Geoffroy *et al.*, 2018; Tiller *et al.*, 2017), which increases the likelihood of export to the seafloor, delivering eDNA to the sediments. It is however not clear whether missing *P. periphylla* DNA in Svalbard sediments verifies a lack of *P. periphylla* in the sampled fjords or is a result of the sampling design. Contrary to *P. periphylla*, *C. capillata* was detected using both net catches and eDNA metabarcoding (**Table 6**), though the results did not match completely. At one station specimens were caught with nets, but no DNA was detected (station 21) while at some stations without *C. capillata* net catches, eDNA was detected (stations 06 & 13). Similarly, the rest of the zooplankton community was also poorly represented by the metabarcoding. Many of the species caught with nets were not detected with the metabarcoding. Since the sorting of the net catches during the HE 560 expedition was focused on GZP and the crustacean taxa *Themisto* and *Thysanoessa*, the net and trawl catches are biased towards Cnidaria and Ctenophora, followed by crustacean zooplankton and pteropods. Other zooplankton groups caught by nets and trawls are prone to biases due to the selective sorting procedure and lack a comprehensive representation. This means that, even though the towing of nets and trawls covers a large water volume, taxa are missed. Overall, the eDNA sampling design might not have been robust enough to give a precise representation of the pelagic communities. It can be assumed that not all DNA is exported to the seafloor and that the sporadic sampling of sediment does not have a high enough spatial resolution to accurately depict the pelagic community. What can be seen with the metabarcoding of the eDNA sediments is that at most stations, the pelagic DNA is dominated by Arthropoda (**Figure 8**). This is mostly the contribution of copepods, which are typically

described the main zooplankton taxa (Svensen *et al.*, 2019; Walkusz *et al.*, 2003). At some stations (stations 02, 06, 24) Cnidaria notably make up most of the reads of the pelagic taxa (> 50 %; **Figure 8**). This indicates that jellyfish might be an important part of pelagic export, which has only rarely been reported thus far (e.g., Lalande & Fortier, 2011). Nevertheless, eDNA studies on other scyphozoan jellyfish show, that their DNA is better preserved, and they likely shed more eDNA than other taxa such as fish (Allan *et al.*, 2021; Minamoto *et al.*, 2017; Ogata *et al.*, 2021), which could contribute to the dominance jellyfish eDNA at some stations. It is however important to note, that RRAs need to be interpreted with caution. They are biased by the binding success of the primers, which can be a problem for some jellyfish species. A prominent example of such issues are Ctenophora, which are often difficult to successfully amplify with standard COI primers (Bucklin *et al.*, 2021). Therefore, assumptions on ctenophore diversity, an important group of the gelatinous zooplankton, cannot be made with metabarcoding using the COI region.

In our study, we analysed eDNA obtained from sediment samples instead of water samples, because it has been shown that sedimentary eDNA concentrations are higher than aqueous eDNA concentrations and show no significantly different species compositions (Sakata *et al.*, 2020; Takasu *et al.*, 2019; Turner *et al.*, 2015). The use of sediment samples does however also bring challenges. The eDNA sediment samples were taken in triplicates, which were in close proximity to each other. They were therefore pooled and regarded as one sample, making them effectively point samples in this analysis. Therefore, the amount of sediment sampled was small and did not cover a large area. Even in replicates taken just a few centimetres apart, differences in the amplified DNA could be observed (A. Murray, personal communication). It is very likely that not all taxa present in the water column are represented in the sedimentary eDNA. Especially species with a patchy distribution might be missed by a small sampling radius. Jellyfish, which are passively drifting with currents, are often highly dispersed and patchily distributed, forming large aggregations according to hydrographic features (Purcell, 2009). Hence their representation in eDNA samples can also be expected to be patchy. Sedimentary eDNA can also be biased towards benthic organisms, as the DNA found in and on sediments is dominated by benthic organisms (Brandt *et al.*, 2021). In our study only 241009 out of 10927605 total reads were from definite pelagic taxa (~ 2 %), thus only the more abundant species may be picked up in the analysis. Another challenge of eDNA studies is the possible dispersal of the eDNA due to hydrodynamics. In marine environments eDNA has been found to be relatively spatially constraint (Eble *et al.*, 2020). This is however caused by the material being quickly reduced below a detectable threshold (Eble *et al.*, 2020; Thomsen & Willerslev, 2015), which allows for detection only close to its source but limits the detection success if only a small scale is observed. Alongside the problem of dispersal caused

by water currents and hydrography, there is also the question of degradation. eDNA, just like particulate organic matter is degraded over time (Collins *et al.*, 2018; Dell'Anno & Corinaldesi, 2004). Even though cold water is known to slow this process (Strickler *et al.*, 2015), it still significantly decreases the amount of material reaching the sea floor. Our study possibly indicates the positive effect of cold temperatures on eDNA preservation. In the West Svalbard fjords mostly influenced by warmer Atlantic water (stations 13 – 25), the number of reads were almost three times less than in North Svalbard fjords (stations 01 – 06), mostly influenced by cold Arctic waters (**Figure 7**). Station 22, which showed reads comparable to stations 01 – 06 (> 1.5 million), is located in Billefjorden in West Svalbard but was characterized by cold water temperatures compared to the other Svalbard fjords (bottom temperature - 1.8 °C, other West Svalbard fjords between 0.87 and - 1.12 °C). It is also possible that biomass was simply higher in the North Svalbard fjords. Perseverance of eDNA, which is still subject of active research due to the relative novelty of eDNA studies especially in the marine environment, also needs to be considered. In lake sediments, eDNA has been documented to be preserved for thousands of years (Ficetola *et al.*, 2018; Pedersen *et al.*, 2016), which might complicate its use to portray a contemporary picture of communities. Studies on the duration of eDNA persistence in sediments are necessary to resolve this challenge.

Overall, our results show that sediment eDNA can be an effective tool for investigating GZP. We could reveal that Cnidaria seem to be important for export in some areas, making them key parts of the zooplankton community and whole ecosystem. There are also indications that a higher species diversity of jellyfish exists in more Arctic-influenced Svalbard fjords. To give precise conclusions about the role of jellyfish in the pelagic community of Arctic fjords, the sampling design needs to be adjusted for future analyses. Using more sampling stations to depict one fjord would yield a higher spatial resolution. This would help in detecting more species, possibly even those with patchy distributions. It would also be helpful to include multiple genetic markers, as COI has been proven to be a challenging marker for some taxa including Ctenophora and pelagic tunicates (Bucklin *et al.*, 2021). Another consideration would be the coupling of multiple methods such as metabarcoding of sediment samples and water samples. This would help reduce the bias of sedimentary eDNA towards benthic organisms. Additionally, visual analyses and net catches could be included of which the species diversity can be compared with that revealed by eDNA analyses. Lastly, depending on the research question it could be useful to use a quantitative PCR approach instead of metabarcoding, which would generate a higher sensitivity towards a target taxon. Additionally, it has the potential to assess the detected eDNA quantitatively, which could be used to assess relative abundances of jellyfish in certain regions and thus provide information on possible blooms.

4.2.2 North Svalbard vs. West Svalbard fjords

When comparing the species diversity of North Svalbard fjords with West Svalbard fjords, which differ in major hydrographic influence, clear differences could be found. In the nMDS model (**Figure 9**) the stations from the northern fjords clustered together, as did the samples from the western fjords, with the former showing a higher variance between the samples. These differences in metazoan species composition were expected, as environmental conditions differ significantly between western fjords more influenced by the Atlantic regime (West Spitsbergen Current) and those influenced by cold Arctic water in the North of Svalbard (Cottier *et al.*, 2018; Gluchowska *et al.*, 2016; Promińska *et al.*, 2017; Skogseth *et al.*, 2020). Other studies showed clear differences in zooplankton community structures between contrasting Svalbard fjords as well. In a study by Weydmann-Zwolicka *et al.* (2021), zooplankton from Kongsfjorden (West Svalbard, Atlantic water) and Rijpfjorden (North Svalbard, Arctic water) was investigated using sediment traps. They found clear differences in species composition in spring and summer, mostly attributed to differences in water temperatures and sedimentation rates. The differences in sea ice coverage in spring and early summer was a major differentiation factor for the zooplankton community structures between the two fjords. Since our samples were collected in summer 2020, we can expect similar effects in our study. Clear differences in pelagic species diversity are revealed in our study. Focusing on the Cnidaria, we can see a higher species diversity in the north compared to the west. This trend is also reflected in the net and trawl catches at the same stations. These results are in line with findings of Mańko *et al.* (2020), where Multinet catches revealed a higher diversity of GZP in Arctic water masses (up to 8 species) compared to Atlantic water (up to 3 species). They attributed geographic factors such as bathymetric zone and sampling depth but also distribution of water masses with the GZP diversity. The higher diversity in the Arctic Water may however be explained by the greater depth of the Arctic waters and entailing higher possibility to find mesopelagic species. Since our study did not characterize bathymetry and water masses, we cannot directly attribute higher diversity to those factors, although an influence of hydrography on species diversity seems likely and has been shown for zooplankton communities in different Svalbard fjords before (Ormańczyk *et al.*, 2017). Mańko *et al.* (2020) also reported that the hydrozoan *Aglantha digitale* was the main contributor to the GZP in Atlantic waters, indicating a bloom of the species. This prevalence of *A. digitale* in Atlantic water masses was also reported by other studies (Licandro *et al.*, 2015; Walkusz *et al.*, 2003; Weydmann-Zwolicka *et al.*, 2021) and could position *A. digitale* as an indicator species of Atlantification. Unfortunately, *A. digitale* had to be excluded from the metabarcoding dataset, due to possible tag-jumping caused by the library being run together with a library including trophic metabarcoding of *A. digitale*. Therefore, our study is not able to give any information on the role of the species in the fjords sampled. The high abundances of *A. digitale*

in the Atlantic waters reported by several studies (Licandro *et al.*, 2015; Walkusz *et al.*, 2003; Weydmann-Zwolicka *et al.*, 2021) contributed to overall higher abundances of Cnidaria in Atlantic waters. Increased abundances of Cnidaria in the Atlantic over the past three decades have been reported frequently, often linked to warm and dry periods (e.g., Edwards *et al.*, 2020; Licandro *et al.*, 2015). Our analysis, like any other DNA metabarcoding study, is limited to assessing diversity of GZP rather than quantifying their abundances. Still, RRAs show that two northern fjords and one western fjord are dominated by Cnidaria reads (**Figure 8**), indicating an important role of Cnidaria in those fjords. This must be interpreted with caution though, since RRAs can be subject to primer and amplification biases. Even though the quantitative nature of metabarcoding has been debated, it has increasingly been shown that RRAs can follow biomass or abundance well in some cases (Bucklin *et al.*, 2016; Ershova *et al.*, 2021; Lacoursière-Roussel *et al.*, 2018; Yang *et al.*, 2017). Still some biases may occur, making RRAs not applicable to explain abundances robustly for all taxa. For example, Ctenophora, which are an important component of GZP communities, are not present in our metabarcoding results, even though they were frequently caught in nets and trawls (**Table 6**). This can entirely be explained with primer biases. Moreover, the net catches used in our study do not offer real abundance data, as they were caught with multiple different types of nets that sample different volumes, at different speeds and depths. Thus, the sampling effort of the net catches was not uniform, making it impossible to extrapolate to comparable abundances. There is also the issue of the reference database used, which is a key factor in determining which taxa are detected. In our study, a local reference database, based on the NCBI GenBank database (Bethesda, 2008) was used to assign the OTUs to taxa. Several taxa could not be matched to phylum level (~ 25 %) and were thus excluded from any analyses. This leaves the assumption that some species were overlooked, simply because no reference sequence was available. Especially for GZP, a group which has been overlooked by many zooplankton studies over time (Brotz *et al.*, 2012; Licandro *et al.*, 2015; Purcell, 2009; Yaragina *et al.*, 2022), the public reference databases are sparse. For the species *P. periphylla,* only 27 COI sequences are listed on NCBI GenBank and for *Atolla* spp., a genus of coronate jellyfish, just 5 sequences of two of the eight recognized species of the genus are listed on GenBank. Some ctenophore taxa are even less represented due to challenges associated with amplifying the barcode COI region with the universal primers.

Due to the increased Atlantification, which is already taking place in Svalbard (Polyakov *et al.*, 2017; Spielhagen *et al.*, 2011), it is likely that new species of GZP will enter the Arctic, or that some local species may increase in abundances in the future. This process might have serious consequences on the biodiversity and community structure of Arctic zooplankton. We can already observe higher abundances of GZP and lower species diversity in Atlantic water

masses (**Figure 10**), compared to Arctic water masses (Edwards *et al.*, 2020; Mańko *et al.*, 2020; Weydmann-Zwolicka *et al.*, 2021). An increased inflow of warmer Atlantic water might cause a higher potential of jellyfish blooms and a decreasing GZP diversity, with jellyfish like *A. digitale* or *C. capillata* – likely benefitting from the Atlantification, increasingly dominating the zooplankton. If species such as *C. capillata*, preying on ichthyoplankton, will have more frequent and massive blooms, they can negatively impact local Arctic fish stocks and harm commercial fisheries expanding poleward (Palmieri *et al.*, 2014; Roux *et al.*, 2013; Tiller *et al.*, 2017). Hence, in order to investigate their impact on the food web and entire ecosystems, monitoring tools need to be developed to detect range-shifting and non-indigenous species before they are able to build up large abundances.

4.3 Species-specific detection of scyphozoans

The primer pair for *Cyanea capillata* developed here proved to be a promising tool for species-specific detection in the scope of our analyses. The characteristics of the final primer pair (Cyacap_2_F; Cyacap_2_R) are in line with the optimal parameters. The length of the amplified sequence is 97 bp which is in the optimal range between 50 and 150 bp (Debode *et al.*, 2017). T_M is similar between forward and reverse primers (Cyacap_2_F = 55 °C; Cyacap_2_R = 55.1 °C), which helps to avoid secondary structure formation, such as hairpins (Rodríguez *et al.*, 2015). GC-content is at the lower margin of the set parameters with 40 % (Cyacap_2_F) and 45 % (Cyacap_2_R), but still in the acceptable range of 30 to 80 % often recommended in the literature (Bustin & Huggett, 2017; Rodríguez *et al.*, 2015). When tested with tissue extract of other scyphozoan jellyfish including *C. lamarckii*, *P. periphylla* and *Atolla* spp.*,* the primer pair only amplified the target DNA sequence of *C. capillata* sensu stricto (Cluster 1) on a satisfactory level. Contrarily, out of the eight initially designed primer pairs for *P. periphylla* none could be identified as species-specific. One disadvantage in the design process of the *P. periphylla* primers was the sequence length of the alignment used for the primer construction. Since the universally used Folmer-primers for the COI gene region did not amplify DNA extract of *Periphylla* tissues, the Leray-primers were used. They however amplify a sequence only half the size (313 bp) of the Folmer-fragment (658 bp), drastically reducing the probability of finding unique base sequences suitable for species-specific amplification. Typically, a sequence length of around 1000 bp is recommended for constructing robust primers for qPCR and species-specific detection (Wilcox *et al.*, 2013). This would make the 658 bp long Folmer-fragment too short for robust results as well. However, it is the most commonly found COI sequence for most metazoan on public databases which gives it the advantage of providing a large sample for the initial alignment. Therefore, the shorter sequence length is a worthwhile trade-off, as the large sample coverage increases the chance of finding a reasonable quality primer pair. The eventual goal of having a species-specific primer for large scyphozoan species like *C. capillata* or *P. periphylla* is to have a robust monitoring tool for the occurrence and potential distributional shifts of the species, which can serve to apply as precautionary measures for fisheries and aquaculture. Therefore, the primers must reliably amplify their DNA when present in environmental samples. When tested in a simulated eDNA experiment (**Figure 4**), Cyacap_2 primers successfully picked up the target DNA sequence. In the application of the primers on sediment DNA extract, they picked up *C. capillata* in 70 % of the samples where *C. capillata* DNA was found with metabarcoding. Considering the low RRAs of jellyfish DNA found in sediment samples, this is a good success rate. Even in samples with only very few reads detected by the metabarcoding (e.g., 2_2b with 6 reads), the primers successfully detected *C. capillata* DNA. This demonstrates the high sensitivity of the primer pair even at low DNA quantities. In addition, some samples from the sediment DNA extractions

for which the metabarcoding analyses did not reveal any *C. capillata* reads were amplified with the Cyacap_2 primers. This means that either the DNA did not get picked up by the metabarcoding with the Leray-primers, or that our designed primers are not highly specific. Without further testing we can only speculate which of the two possibilities is most likely. The Leray-primers have been proven to be a well-working primer for metabarcoding metazoan taxa including jellyfish like *C. capillata* (van den Heuvel-Greve *et al.*, 2021; Leray *et al.*, 2013). These findings are also in line with previous tests on our part, which showed a 100 % success rate of the Leray-primers for *C. capillata*. Its relatively short size also makes it a good marker for environmental DNA (Bakker *et al.*, 2019), as eDNA is often degraded and thus shorter than DNA extracted directly from the organisms (Barnes *et al.*, 2014; Collins *et al.*, 2018). As the fragment amplified by our own primer pair is even shorter than the Leray-fragment, it increases the possibility of DNA still being detectable in an environmental sample (Jo *et al.*, 2019; Saito & Doi, 2021). There were also many unassigned OTUs in the sediment dataset, so it is not possible to rule out the possibility of *C. capillata* DNA being missed by the metabarcoding approach. Other studies also show the problem of cnidarian OTUs being rarely assigned below the class or order level using COI (Wangensteen *et al.*, 2018). The high diversity we recovered within *C. capillata* sensu lato could for example lead to the species not being annotated in some cases. To better understand their specificity and efficiency, sensitivity assays of both primers are necessary, by applying a matrix using decreasing concentrations of target DNA in a PCR. This would show if our newly designed primer pair is more sensitive to low DNA concentrations than the universal Leray-primers. A more robust specificity testing would be necessary to rule out the possibility of other OTUs being picked up by the primer. Alternatively, all samples where a band was seen could be Sanger sequenced to check whether *C. capillata* can be identified. Since we only included a limited number of scyphozoan species in our tests, it may be that other OTUs were detected with our primer, explaining the higher number *C. capillata* detections by the primers compared to the metabarcoding reads. A more robust test would include not only related species (e.g., other Cnidaria) but also species co-existing in the same habitat and potential contaminants (e.g., humans). It might also be beneficial to apply the primers on mock communities of known composition to test whether other species will be detected. This testing would however need to be adapted to the research goal. If the scope is to detect jellyfish as a measure of precaution before they bloom, it might be necessary to further test the primer on water samples. Because the jellyfish DNA would take several days to reach the sediments (Collins *et al.*, 2018), this would give a more immediate result of a bloom. To detect range shifts or non-indigenous species, sediment samples might be more useful as eDNA seems to preserve better in sediments and is not as easily dispersed. This would be more telling on whether a species has established itself in a new habitat, rather than if its DNA being advected there.

Generally, our *C. capillata* specific primers show a high potential of being used as basis for a species-specific monitoring tool for *C. capillata*, e.g., using a qPCR assay. Here the next steps for developing a rapid-detection tool based on a qPCR approach will briefly be described. After successfully testing specificity and sensitivity of the primers in a normal PCR, they would need to be optimized for qPCR. Firstly, positive and negative controls, known from the normal PCR testing beforehand, would be tested in the qPCR. Then, cross-amplification would be tested by using related species, possible contaminants, and species co-existing in the same habitat. Lastly, the primer concentrations in the qPCR master mix would be optimized. For this, a matrix could be applied, testing different concentrations of both forward and reverse primer against each other. Once the specificity of the primers is tested and the optimal concentrations for the qPCR are found, standard curves can be created to be able to make quantitative conclusions. If these tests are carried out successfully, the newly developed primer pair for *C. capillata* (Cyacap_2_F; Cyacap_2_R) would make a strong detection tool for monitoring the species in areas where blooms could be increasingly expected with rising sea temperatures. This could help to develop precautionary measures for jellyfish blooms which can otherwise be harmful to local fisheries and aquaculture.

4.4 Conclusion

Overall, our results are informative in the context of the hypothesized jellification and range shifts of Atlantic species into the Arctic. The genetic connectivity analyses show a high genetic homogeneity for both *P. periphylla* and *C. capillata* populations. Our phylogeographic results may be an indication of a population connectivity due to recent gene flow over large distances. Especially *P. periphylla* lacks genetic structure of its geographic populations and shows a moderate diversity, both suggesting genetic mixing, which produces identical haplotypes over a wide latitudinal gradient. On the other hand, *C. capillata* shows a high genetic diversity with three species-level lineages being uncovered. This demonstrates how poorly understood the species still is and how crucial further investigation will be to understand possible range shifts. Generally, a better understanding of the distributions of different scyphozoan lineages, their niches and ecology, and their impact is necessary. The application of faster-evolving genetic markers, like SNPs or microsatellites, will be necessary to further explore the observed patterns and provide a detailed demographic history. High genetic diversity is the motor of adaptation and can in turn increase the probability of establishment of a species in a new habitat or cause an increase in abundance of locally established populations under changing climate scenarios. As of today, it seems that there is not yet a troublesome development of jellyfish taking place in the high Arctic. However, as cnidarian blooms can have negative impacts on local fisheries and aquacultures, it is important to study how their populations change over time. Our metabarcoding results reveal that jellyfish DNA only makes up a small part of the overall DNA exported to the seafloor. However, in some fjords, the pelagic community observed with our methods seems to be dominated by jellyfish. Furthermore, a higher Cnidarian diversity was found in North Svalbard fjords, compared to West Svalbard fjords. With more Arctic fjords expected to become impacted by Atlantification, it is important to further investigate these patterns to predict shifts in GZP diversity and abundances. In order to identify shifts in the GZP community structure, tools for a rapid detection of key species should be developed. Our newly designed primer pair, specific for *C. capillata,* provide the baseline for such studies. The primer successfully amplified DNA from tissue extract and environmental DNA extracts from water and sediment samples. With the laid-out adaptations and tests, it will make a powerful, cost-effective detection method to quantitively assess *C. capillata* eDNA. Furthermore, the same method could be applied to other scyphozoan species in the Arctic, in particular those that are likely to interfere with human activity or ecosystem services. With our study, we show the major potential of modern molecular tools for investigating jellyfish range shifts and lay the framework for future monitoring studies based on eDNA.

VI References

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VIII Appendix

Appendix 1 Sampling information for all jellyfish individuals used for DNA barcoding and primer testing.

Cruise	Station	Longitude	Latitude	Sampling Gear	DNA [ng/µL]	Sample-ID	Species
WH 440	710	65,4938	-30,2520	BT140	17,22	JF_011	*Atolla* spp.
WH 440	713	65,5508	-32,4490	BT140	12,19	JF_025	*Atolla* spp.
WH 440	713	65,5508	-32,4490	BT140	4,08	JF_026	*Atolla* spp.
WH 440	716	65,4305	-32,7400	BT140	6,70	JF_031	*Atolla* spp.
WH 440	719	-34,1608	65,1012	BT140	301,61	JF_0037	*P. periphylla*
WH 440	719	-34,1608	65,1012	BT140	651,45	JF_0038	*P. periphylla*
WH 440	719	-34,1608	65,1012	BT140	2310,26	JF_0039	*P. periphylla*
WH 440	725	-35,1825	64,4522	BT140	232,17	JF_0044	*P. periphylla*
WH 440	725	-35,1825	64,4522	BT140	502,61	JF_0046	*P. periphylla*
WH 440	727	-35,1090	64,6572	BT140	438,97	JF_0052	*P. periphylla*
WH 440	727	-35,1090	64,6572	BT140	148,07	JF_0053	*P. periphylla*
WH 440	727	-35,1090	64,6572	BT140	368,60	JF_0055	*P. periphylla*
WH 440	728	-35,0992	64,7152	BT140	21,23	JF_057	*Atolla* spp.
WH 440	728	-35,0992	64,7152	BT140	1347,66	JF_0058	*P. periphylla*
WH 440	728	-35,0992	64,7152	BT140	305,76	JF_0059	*P. periphylla*
WH 440	731	-36,5832	63,8555	BT140	261,70	JF_0060	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	190,63	JF_0063	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	491,57	JF_0065	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	756,81	JF_0066	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	717,25	JF_0067	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	763,22	JF_0068	*P. periphylla*
WH 440	732	-36,5285	63,8652	BT140	217,45	JF_0069	*P. periphylla*
WH 440	733	-36,3343	63,9900	BT140	452,67	JF_0070	*P. periphylla*
WH 440	733	-36,3343	63,9900	BT140	315,70	JF_0071	*P. periphylla*
WH 440	744	-37,1448	64,4088	BT140	-34,13	JF_080	*C. capillata*
WH 440	746	-37,1885	64,4490	BT140	408,69	JF_0081	*P. periphylla*
WH 440	754	-38,3863	63,5443	BT140	169,46	JF_0098	*P. periphylla*
WH 440	754	-38,3863	63,5443	BT140	257,62	JF_0099	*P. periphylla*
WH 440	757	-39,1630	63,5953	BT140	178,17	JF_0102	*P. periphylla*
WH 440	757	-39,1630	63,5953	BT140	662,97	JF_0103	*P. periphylla*
WH 440	757	-39,1630	63,5953	BT140	458,75	JF_0104	*P. periphylla*
WH 440	758	-39,0433	63,4668	BT140	376,75	JF_0105	*P. periphylla*
WH 440	758	-39,0433	63,4668	BT140	389,12	JF_0107	*P. periphylla*
WH 440	758	-39,0433	63,4668	BT140	194,36	JF_0110	*P. periphylla*
WH 440	758	-39,0433	63,4668	BT140	152,65	JF_0112	*P. periphylla*
WH 440	758	-39,0433	63,4668	BT140	426,63	JF_0113	*P. periphylla*
WH 440	762	-40,5975	62,5363	BT140	230,11	JF_0114	*P. periphylla*
WH 440	762	-40,5975	62,5363	BT140	309,00	JF_0115	*P. periphylla*
WH 440	762	-40,5975	62,5363	BT140	159,58	JF_0116	*P. periphylla*
WH 440	762	-40,5975	62,5363	BT140	1200,74	JF_0117	*P. periphylla*
WH 440	762	-40,5975	62,5363	BT140	291,65	JF_0118	*P. periphylla*
WH 440	763	-40,7548	62,5323	BT140	306,98	JF_0119	*P. periphylla*
WH 440	767	-40,4917	62,4908	BT140	125,86	JF_124	*Atolla* spp.
WH 440	767	-40,4917	62,4908	BT140	560,08	JF_0127	*P. periphylla*
WH 440	770	-40,8092	62,1340	BT140	892,29	JF_0127	*P. periphylla*
WH 440	770	-40,8092	62,1340	BT140	835,54	JF_0128	*P. periphylla*
WH 440	770	-40,8092	62,1340	BT140	477,97	JF_0129	*P. periphylla*

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Appendix 1 (continued)

WH 440	770	-40,8092	62,1340	BT140	673,89	JF_0130	*P. periphylla*
WH 440	779	-44,9082	59,7190	BT140	471,22	JF_0141	*P. periphylla*
WH 440	785	-50,4045	62,2235	BT140	778,78	JF_0142	*C. capillata*
WH 440	785	-50,4045	62,2235	BT140	169,19	JF_0144	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	389,44	JF_0145	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	480,80	JF_0146	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	669,64	JF_0147	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	401,06	JF_0148	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	298,45	JF_0149	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	172,55	JF_0150	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	197,83	JF_0151	*P. periphylla*
WH 440	789	-50,6128	62,0275	BT140	318,93	JF_0152	*P. periphylla*
WH 440	790	-50,6308	62,0930	BT140	425,49	JF_0154	*P. periphylla*
WH 440	804	-54,5993	64,7633	BT140	-29,39	JF_0174	*C. capillata*
WH 440	804	-54,5993	64,7633	BT140	-179,02	JF_0175	*C. capillata*
WH 440	804	-54,5993	64,7633	BT140	369,60	JF_0177	*P. periphylla*
WH 440	805	-54,5993	64,7633	BT140	-26,54	JF_0178	*C. capillata*
WH 440	805	-54,5993	64,7633	BT140	1155,23	JF_0179	*P. periphylla*
WH 440	806	-54,3785	64,8553	BT140	197,69	JF_0181	*P. periphylla*
WH 440	806	-54,3785	64,8553	BT140	200,75	JF_0182	*C. capillata*
WH 440	806	-54,3785	64,8553	BT140	279,61	JF_0183	*P. periphylla*
WH 440	806	-54,3785	64,8553	BT140	929,14	JF_0184	*P. periphylla*
WH 440	806	-54,3785	64,8553	BT140	169,98	JF_0186	*P. periphylla*
WH 440	807	-54,5993	64,7633	BT140	-30,80	JF_0187	*C. capillata*
WH 440	807	-54,5993	64,7633	BT140	465,50	JF_0188	*P. periphylla*
WH 440	807	-54,5993	64,7633	BT140	499,51	JF_0190	*P. periphylla*
WH 440	807	-54,5993	64,7633	BT140	1178,54	JF_0191	*P. periphylla*
WH 440	826	-53,1208	63,9957	BT140	773,25	JF_0248	*P. periphylla*
WH 440	813	-55,9463	66,4853	BT140	-20,20	JF_0222	*C. capillata*
WH 440	813	-55,9463	66,4853	BT140	319,34	JF_0224	*P. periphylla*
WH 440	815	-55,9463	66,4853	BT140	-2,71	JF_0225	*C. capillata*
WH 440	815	-55,9463	66,4853	BT140	-16,14	JF_0226	*C. capillata*
WH 440	815	-55,9463	66,4853	BT140	-11,66	JF_0227	*C. capillata*
WH 440	817	-55,9463	66,4853	BT140	1,08	JF_0228	*C. capillata*
WH 440	817	-55,9463	66,4853	BT140	-1,21	JF_0229	*C. capillata*
WH 440	818	-55,9463	66,4853	BT140	-1,14	JF_0230	*C. capillata*
WH 440	821	-54,5993	64,7633	BT140	264,28	JF_0232	*C. capillata*
WH 440	821	-54,5993	64,7633	BT140	-23,55	JF_249	*C. capillata*
WH 440	823	-54,5993	64,7633	BT140	-30,15	JF_250	*C. capillata*
HE 560	2	22,1540	80,1787	Pelagic_3	275,21	CY174	*C. capillata*
HE 560	2	22,1540	80,1787	Pelagic_3	186,43	CY175	*C. capillata*
HE 560	4	19,6496	79,5218	ShallowQ	12,48	CY178	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/6	486,84	CY416	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/6	27,67	CY417	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/6	774,15	CY418	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/7	27,34	CY419	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/7	21,04	CY420	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/7	68,25	CY421	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/7	253,25	CY422	*C. capillata*
HE 560	8	13,0775	79,6448	YFT 8/7	336,73	CY423	*C. capillata*

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Appendix 1 (continued)

HE 560	8	13,0775	79,6448	YFT 8/7	460,44	CY424	*C. capillata*
HE 560	10	12,0405	79,7951	Shallow Q	405,78	CY428	*C. capillata*
HE 560	10	12,0405	79,7951	YFT 10/7	61,55	CY448	*C. capillata*
HE 560	10	12,0405	79,7951	YFT 10/7	321,58	CY449	*C. capillata*
HE 560	10	12,0405	79,7951	YFT 10/8	27,80	CY451	*C. capillata*
HE 560	10	12,0405	79,7951	YFT 10/8	1356,56	CY452	*C. capillata*
HE 560	11	11,0922	79,7142	YFT 11/8	193,90	CY492	*C. capillata*
HE 560	12	8,9813	79,4365	YFT 12/8	25,27	CY511	*C. capillata*
HE 560	15	10,2405	79,0202	BT 15/8	-258,62	CY577	*C. capillata*
HE 560	17	11,7370	79,1702	YFT 17/8	39,79	CY616	*C. capillata*
HE 560	21	10,5906	77,4333	YFT 21/8	34,07	CY713	*C. capillata*
HE 560	23	16,6751	78,6578	Deep NQ	381,51	CY748	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/3	46,18	CY774	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/3	399,69	CY775	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/3	-18,63	CY776	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/3	238,58	CY777	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/3	12,19	CY778	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/4	-14,95	CY779	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/4	130,25	CY780	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/4	-45,76	CY781	*C. capillata*
HE 560	23	16,6751	78,6578	YFT 23/5	719,31	CY782	*C. capillata*
HE 570	M7	5,3938	60,8722	Multinet maxi	173,84	Ppe_01	*P. periphylla*
HE 570	L7	5,1550	60,6922	On top Rosina	33,50	Ppe_02	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet midi	52,84	Ppe_03	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	38,85	Ppe_09	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	48,53	Pp_13	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	13,68	Ppe_18	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	10,54	Ppe_19	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	74,43	Ppe_23	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	15,60	Ppe_24	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	38,54	Ppe_26	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	19,55	Ppe_30	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	50,19	Ppe_37	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	17,34	Ppe_45	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	18,31	Ppe_46	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	95,14	Ppe_51	*P. periphylla*
HE 570	L7	5,1550	60,6922	Multinet maxi	113,72	Ppe_53	*P. periphylla*
KOP-183	Wharf-4	11,9346	78,9287	Hand net	14,54	JEL260/ PerZ001	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL274/ CyZ001	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL275/ CyZ002	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL276/ CyZ003	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL277/ CyZ004	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL278/ CyZ005	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL279/ CyZ006	*C. capillata*
KOP-183	Wharf-5	11,9346	78,9287	Hand net		JEL280/ CyZ007	*C. capillata*

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Appendix 1 (continued)

KOP-183	Wharf-5	11,9346	78,9287	Hand net	6,81	JEL299/ PerZ002	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	43,39	JEL300/ PerZ003	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	45,09	JEL301/ PerZ004	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	26,70	JEL302/ PerZ005	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	13,35	JEL303/ PerZ006	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	56,73	JEL304/ PerZ007	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	46,25	JEL305/ PerZ008	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	24,71	JEL306/ PerZ009	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	30,97	JEL307/ PerZ010	*P. periphylla*
KOP-183	Wharf-5	11,9346	78,9287	Hand net	90,11	JEL308/ PerZ011	*P. periphylla*
PS126	HG-IX	2,8450	79,1353	Multinet maxi	43,67	IND1329	*Atolla* spp.
PS122/5	62-118	107,2582	89,0663	RN150_1	79,84	00636	*Atolla* spp.
8 Ephyrae from Culture (S. Holst), Polyps reared from Medusa Helgoland 2020					11,47	–	*C. lamarckii*

Appendix 2 Sampling information of all sediment samples used in the eDNA metabarcoding analyses.

Station	Device	Depth (m)	Longitude	Latitude	Sample replicates (1 – 3)	PCR replicates (a – c)
HE560_1-2	Grab	244	22,0578	80,5193	3	3
HE560_6-2	Grab	228	16,0245	79,1265	3	3
HE560_10-3	Multi Corer	215,6	12,0115	79,8045	3	3
HE560_15-3	Multi Corer	318,6	10,7454	79,0189	3	3
HE560_21-2	Grab	1183,2	10,5470	77,4999	3	3
HE560_21-3	Multi Corer	1170,8	10,5605	77,5020	3	3
HE560_22-4	Multi Corer	184,5	16,6762	78,6591	3	3
HE560_24-2	Grab	100,5	15,1260	77,7640	3	3
HE560_25-3	Multi Corer	122,8	16,4419	76,9962	3	3

Appendix 3 GenBank Accession numbers and locality of sample of all *C. capillata* individuals used in the construction of the NJ-tree. Identical sequences are grouped by boxes.

Accession Nr.	Locality	Latitude	Longitude	bp	References
AY902911.1	Northeast Atlantic			657	Dawson ()
HF930525.1	Northeast Atlantic			658	Armani (2013)
HF930526.1	Northeast Atlantic			658	Armani (2013)
JX995330.1	Baltic Sea	55,2574	9,7069	658	Holst & Laakmann (2013)
JX995331.1	Baltic Sea	55,2574	9,7069	658	Holst & Laakmann (2013)
JX995333.1	Baltic Sea	55,2574	9,7069	658	Holst & Laakmann (2013)
JX995334.1	Baltic Sea	55,2574	9,7069	658	Holst & Laakmann (2013)
JX995335.1	North Sea	54,1863	7,9000	658	Holst & Laakmann (2013)
JX995336.1	North Sea	54,1863	7,9000	658	Holst & Laakmann (2013)
JX995337.1	North Sea	54,1863	7,9000	658	Holst & Laakmann (2013)
JX995338.1	North Sea	54,1863	7,9000	658	Holst & Laakmann (2013)
JX995339.1	North Sea	54,1863	7,9000	658	Holst & Laakmann (2013)
JX995340.1	Northeast Atlantic	67,6333	-12,1667	658	Holst & Laakmann (2013)
JX995341.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
JX995342.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
JX995343.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
JX995332.1	Baltic Sea	55,2574	9,7069	658	Holst & Laakmann (2013)
JX995344.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
JX995345.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
JX995346.1	Baltic Sea	54,4352	10,1701	658	Holst & Laakmann (2013)
KM281972.1	White Sea	66,34	33,0800	714	Kolbasova *et al.* (2015)
KM281978.1	White Sea	66,34	33,0800	715	Kolbasova *et al.* (2015)
KM983293.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM281973.1	White Sea	66,34	33,0800	725	Kolbasova *et al.* (2015)
KM281974.1	White Sea	66,34	33,0800	712	Kolbasova *et al.* (2015)
KM281975.1	White Sea	66,34	33,0800	713	Kolbasova *et al.* (2015)
KM281979.1	White Sea	66,34	33,0800	715	Kolbasova *et al.* (2015)
KM281980.1	White Sea	66,34	33,0800	713	Kolbasova *et al.* (2015)
KM281981.1	White Sea	66,34	33,0800	714	Kolbasova *et al.* (2015)
KM281982.1	White Sea	66,34	33,0800	715	Kolbasova *et al.* (2015)
KM281983.1	White Sea	66,34	33,0800	714	Kolbasova *et al.* (2015)
KM281984.1	White Sea	66,34	33,0800	708	Kolbasova *et al.* (2015)
KM281988.1	White Sea	66,34	33,0800	714	Kolbasova *et al.* (2015)
KM281991.1	White Sea	66,34	33,0800	713	Kolbasova *et al.* (2015)
KM281992.1	White Sea	66,34	33,0800	713	Kolbasova *et al.* (2015)
KM281996.1	White Sea	66,34	33,0800	715	Kolbasova *et al.* (2015)
KM983282.1	White Sea	66,55379	33,10473	654	Kolbasova *et al.* (2015)
KM983283.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM983284.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)

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Appendix 3 (continued)

KM983285.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM983287.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM983291.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM983292.1	White Sea	66,55379	33,10473	657	Kolbasova *et al.* (2015)
KM281976.1	White Sea	66,34	33,0800	714	Kolbasova *et al.* (2015)
KM281977.1	White Sea	66,34	33,0800	611	Kolbasova *et al.* (2015)
KM281986.1	White Sea	66,34	33,0800	708	Kolbasova *et al.* (2015)
KM281989.1	White Sea	66,34	33,0800	677	Kolbasova *et al.* (2015)
KM281995.1	White Sea	66,34	33,0800	726	Kolbasova *et al.* (2015)
MF141607.1	Northeast Atlantic			616	Bayha *et al.* (2017)
MG421412.1	Northwest Atlantic	58,792	-93,751	658	Dewaard, J.R. (unpublished)
MG421494.1	Northwest Atlantic	58,8556	-94,23	640	Dewaard, J.R. (unpublished)
MG421890.1	Northwest Atlantic	44,956	-66,9278	637	Dewaard, J.R. (unpublished)
MG423233.1	Northwest Atlantic	58,875	-93,8004	658	Dewaard, J.R. (unpublished)
MG423329.1	Northwest Atlantic	58,792	-93,751	658	Dewaard, J.R. (unpublished)
MG935310.1	North Sea	58,350	11,222	658	Lundin, K.G. (unpublished)
MH087506.1	Northwest Atlantic	38,8832	-76,5468	658	Anguilar *et al.*, (unpublished)
MH087560.1	Northwest Atlantic	38,8763	-76,5465	658	Anguilar *et al.*, (unpublished)
MH087579.1	Northwest Atlantic	38,8856	-76,542	658	Anguilar *et al.*, (unpublished)
MH087614.1	Northwest Atlantic	38,8832	-76,5468	658	Anguilar *et al.*, (unpublished)
MH087645.1	Northwest Atlantic	38,8832	-76,5468	647	Anguilar *et al.*, (unpublished)
MH087647.1	Northwest Atlantic	38,8763	-76,5465	658	Anguilar *et al.*, (unpublished)

Appendix 4 GenBank Accession numbers of all *C. lamarckii*, *P. periphylla* and *Atolla* spp. individuals used in the alignment for the primer-design process.

Accession Nr.	species	bp	References
MG935374.1	*Cyanea lamarckii*	658	Lundin, K.G., (unpublished)
MG935135.1	*Cyanea lamarckii*	658	Lundin, K.G., (unpublished)
HF930524.1	*Cyanea lamarckii*	658	Armani *et al.*, 2013
HF930523.1	*Cyanea lamarckii*	658	Armani *et al.*, 2013
JX995359.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995358.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995362.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995361.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995360.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995357.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995356.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995355.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995354.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995353.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995352.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995351.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995350.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995349.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995348.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
JX995347.1	*Cyanea lamarckii*	658	Holst & Laakmann, 2013
GQ120088.1	*Atolla wyvillei*	831	Ortman *et al.*, 2010
GQ120087.1	*Atolla wyvillei*	684	Ortman *et al.*, 2010
GQ120086.1	*Atolla wyvillei*	637	Ortman *et al.*, 2010
GQ120085.1	*Atolla vanhoeffeni*	820	Ortman *et al.*, 2010
GQ120084.1	*Atolla vanhoeffeni*	808	Ortman *et al.*, 2010
MF742347.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742346.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742345.1	*Periphylla periphylla*	578	Abboud *et al.*, 2018
MF742344.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742343.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742342.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742341.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742340.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742339.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742338.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742337.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742336.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742335.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742334.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742333.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018

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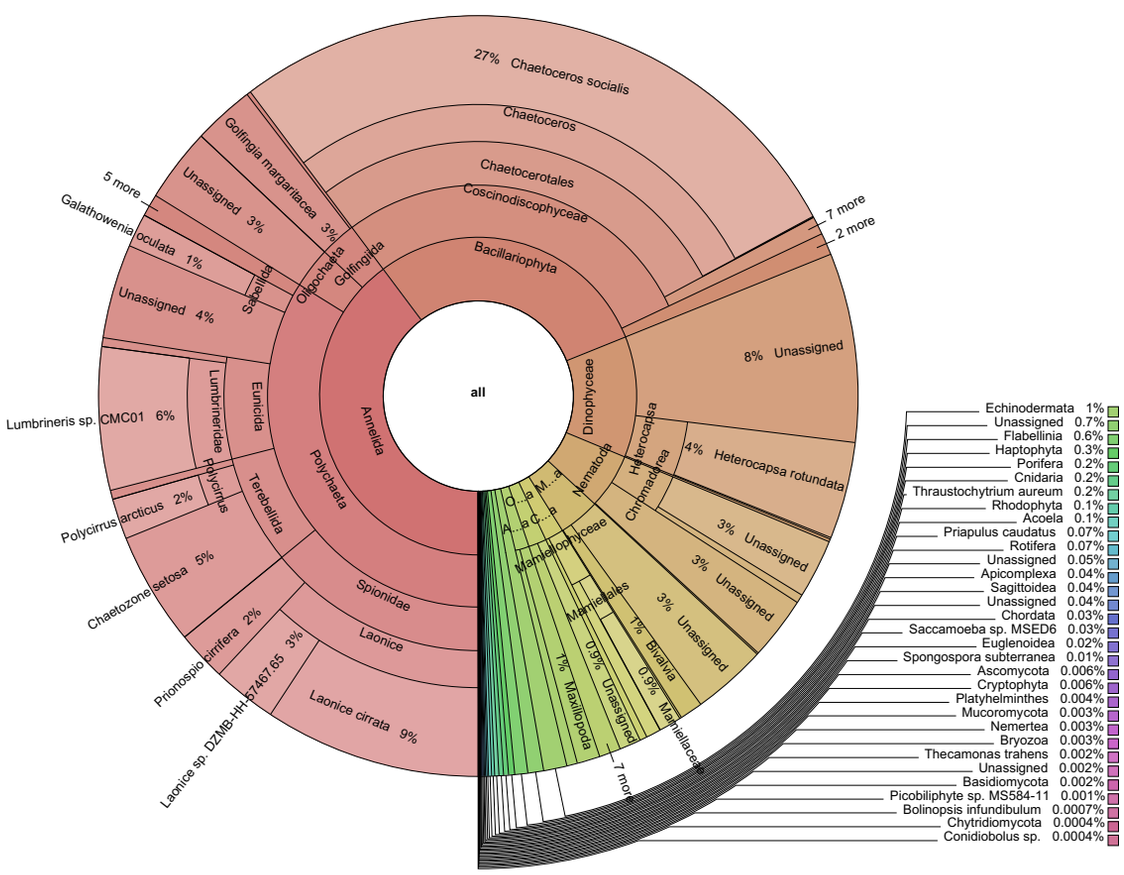
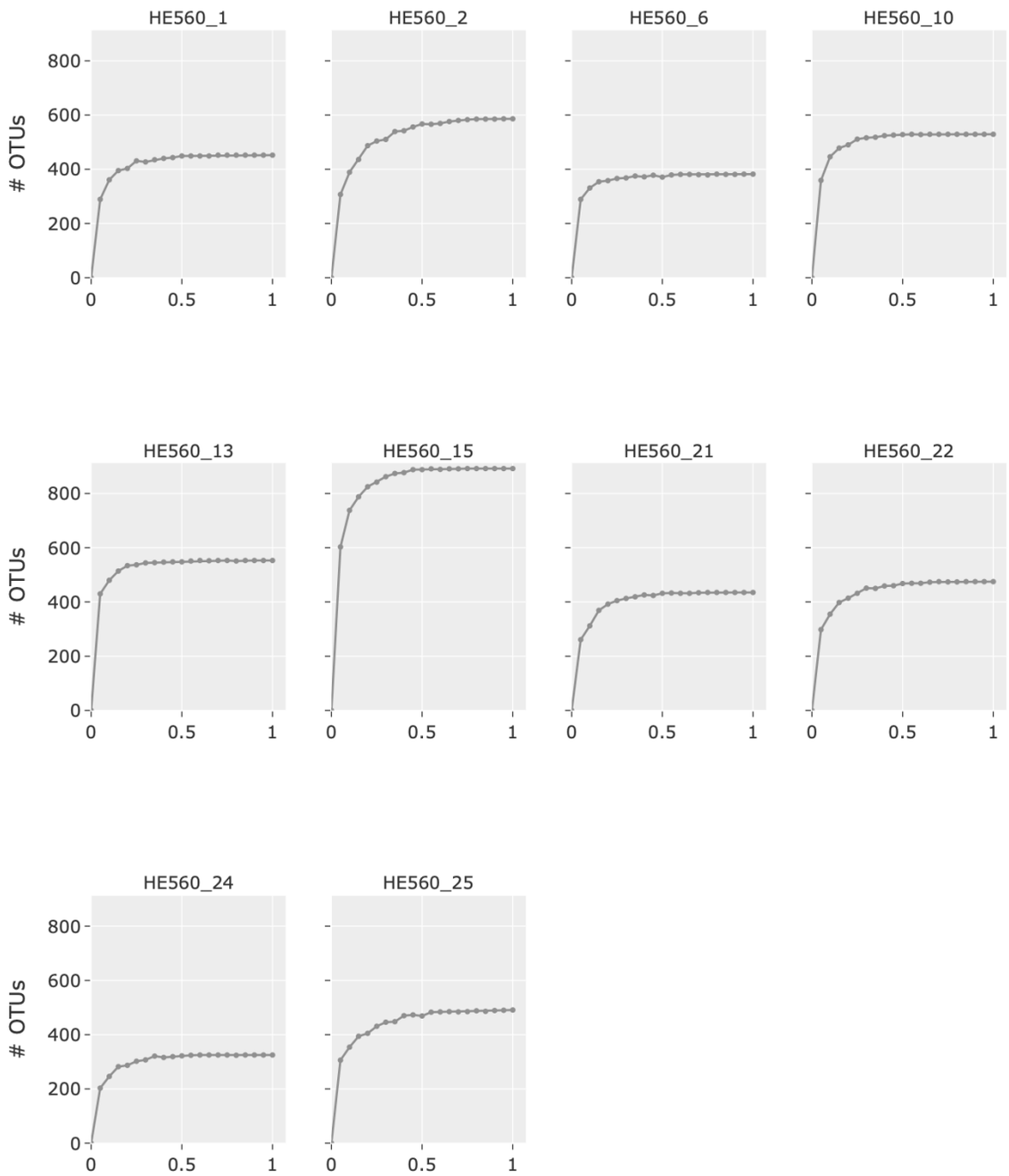
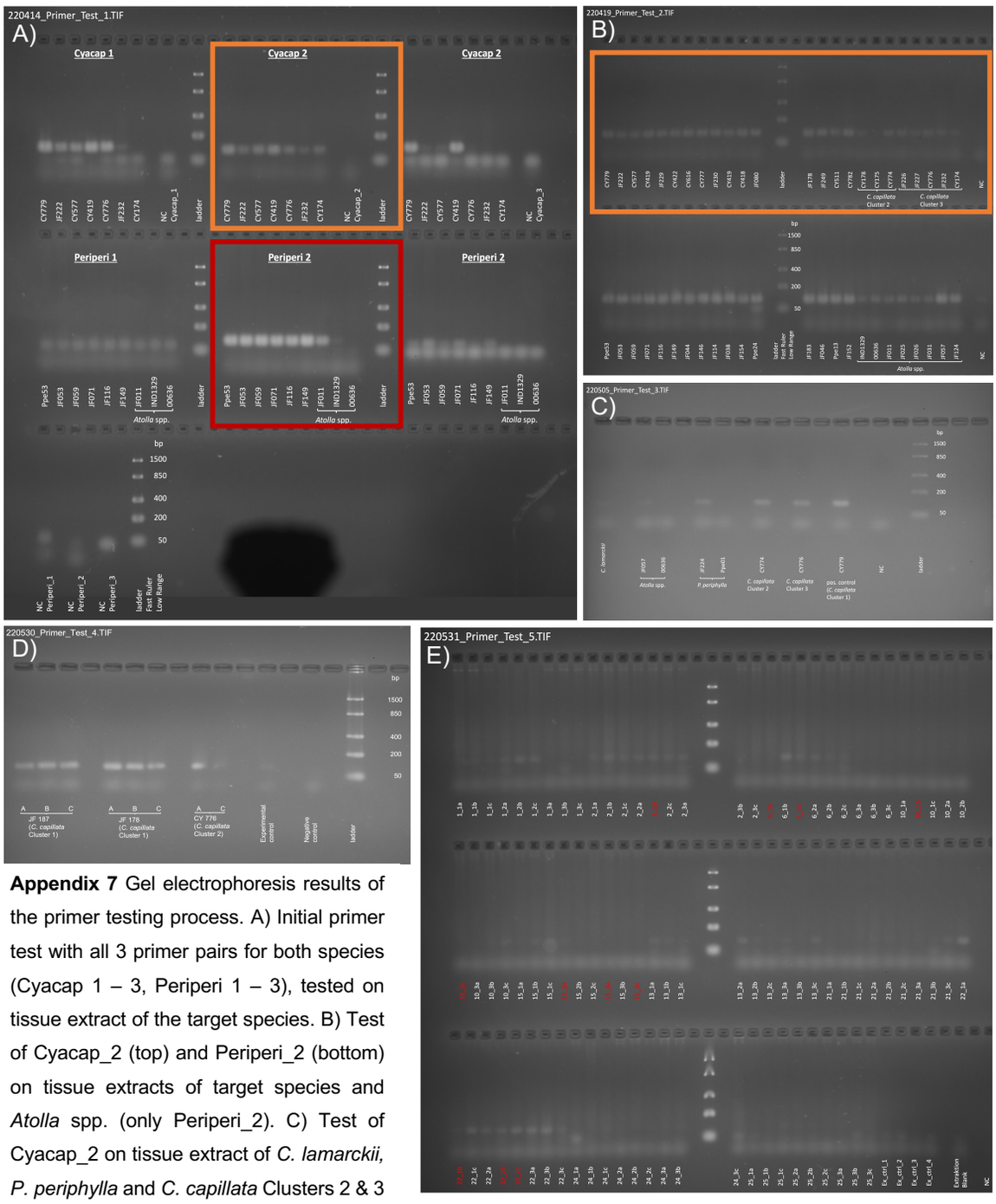
MF742332.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742331.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742330.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742329.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742328.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742327.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742326.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742325.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742324.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742323.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742322.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018
MF742321.1	*Periphylla periphylla*	616	Abboud *et al.*, 2018



Appendix 5 Krona chart showing taxonomic composition of the pooled sediment eDNA dataset from 10 stations around Svalbard (HE 560). OTUs unassigned to the phylum level are not depicted.



Appendix 6 Read-based rarefaction curves of sediment eDNA samples from Svalbard (HE 560). Plotting number of OTUs over reads.



Appendix 7 Gel electrophoresis results of the primer testing process. A) Initial primer test with all 3 primer pairs for both species (Cyacap 1 – 3, Periperi 1 – 3), tested on tissue extract of the target species. B) Test of Cyacap_2 (top) and Periperi_2 (bottom) on tissue extracts of target species and *Atolla* spp. (only Periperi_2). C) Test of Cyacap_2 on tissue extract of *C. lamarckii, P. periphylla* and *C. capillata* Clusters 2 & 3 obtained from NJ-trees. Positive control = *C. capillata* Cluster 1. D) Test of Cyacap_2 on water extract from mesocosm experiment. E) Test of Cyacap_2 on sediment samples from Svalbard. Coloured boxes (orange = *C. capillata*; red = *P. periphylla*) show primers with the best results from each test, that were selected for the next testing step (testing on tissue extract).

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