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Understanding the biodiversity and ecological importance of ctenophores – Lessons from Arctic and Baltic *Mertensia ovum*

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I **Majaneva, S**. & Majaneva, M. 2013: Cydippid ctenophores in the coastal waters of Svalbard: is it only *Mertensia ovum*? – Polar Biology 36: 1681-1686.

II **Lehtiniemi, M**., Gorokhova, E., Bolte, S., Haslob, H., Huwer, B., Katajisto, T., Lennuk, L., Majaneva, S., Põllumäe, A., Schaber, M., Setälä, O., Reusch, T. B. H., Viitasalo-Frösén, S., Vuorinen, I. & Välipakka, P. 2013: Distribution and reproduction of the Arctic ctenophore *Mertensia ovum* in the Baltic Sea – Marine Ecology Progress Series 491: 111-124.

III **Granhag, L**., Majaneva, S. & Møller, L. F. 2012: First recordings of the ctenophore *Euplokamis* sp. (Ctenophora, Cydippida) in Swedish coastal waters and molecular identification of this genus – Aquatic Invasions 7: 455-463.

IV **Majaneva, S**., Berge, J., Renaud, P.E., Vader, A., Stübner, E., Rao, A.M., Sparre, Ø. & Lehtiniemi, M. 2013: Aggregations of predators and prey affect predation impact of the Arctic ctenophore *Mertensia ovum* – Marine Ecology Progress Series 476: 87-100.

V **Majaneva, S**., Setälä, O., Gorokhova, E. & Lehtiniemi, M. 2014: Feeding of the Arctic ctenophore *Mertensia ovum* in the Baltic Sea: evidence of the use of microbial prey. – Journal of Plankton Research 36: 91-103.

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UNDERSTANDING THE BIODIVERSITY AND ECOLOGICAL IMPORTANCE OF CTENOPHORES – LESSONS FROM ARCTIC AND BALTIC *MERTENSIA OVUM*

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Majaneva, S. 2014: Understanding the biodiversity and ecological importance of ctenophores – Lessons from Arctic and Baltic *Mertensia ovum*. – W. & A. de Nottbeck Foundation Sci. Rep. 41: 1–74. ISBN 978-952-67851-5-8 (paperback), ISBN 978-952-67851-6-5 (PDF, http://ethesis.helsinki.fi).

Gelatinous zooplankton, such as ctenophores, have attracted attention during the last decade, mainly as a result of the enigma around their potentially increased abundances around the world. Despite the increased attention, they remain either understudied or disregarded in most food web investigations and monitoring programs, and are defined as one of the most difficult groups of pelagic animals to study. Consequently, their diversity and ecological role are often grossly oversimplified and misunderstood, leading to biased views of ecosystem functioning. In addition, ctenophores share traits such as voracious predation behavior, the ability to starve and shrink during periods of low food availability and to tolerate increased temperatures, as well as high reproductive capacity, making them likely to take advantage of changing environmental conditions.

In the Arctic, earlier ctenophore data consist of sparse abundance estimates and dietary studies lacking a systematic or integrative approach. In the Baltic Sea, despite the well-established routine plankton monitoring program conducted by the surrounding nations, the distribution and the role of the Arctic ctenophore *Mertensia ovum* in this ecosystem has been unknown since its first reported appearance in 2007. In this thesis, the biodiversity of cydippid ctenophores and their role in Svalbard waters and in the Baltic Sea were studied. Extensive *in situ* sampling, laboratory experiments, morphological and molecular identification analysis, traditional and molecular gut content analysis, as well as several direct measures of the ctenophores and the pelagic communities they inhabit were combined to address system-specific questions and to better understand how important a role the ctenophores might have in marine ecosystems.

A combination of morphological species identification and molecular methods revealed *Euplokamis* sp. and an unidentified mertensiid species to co-occur with the dominating *Mertensia ovum* in Arctic waters. Similarly, the first recording of the cydippid ctenophore, *Euplokamis* sp., near the entrance to the Baltic Sea was reported in conjunction with extensive sampling of *Mnemiopsis leidyi* and *Mertensia ovum*. Interestingly, *Pleurobrachia pileus*, earlier reported to commonly co-occur with *M. ovum* in the Arctic and be present throughout the Baltic Sea (and earlier reported as the only ctenophore species in the northern Baltic Sea), was not present in either study site. It was demonstrated that morphological species

identification alone is insufficient. In addition, the lack of proper species descriptions and public sequences limited the identification to the genus, family or order level. Thus, more emphasis should be placed on combining morphological and molecular methods together with photographic vouchers for rigorous taxonomic identification and accurate species descriptions.

The lack of historical survey data and accurate abundance estimates of *M. ovum* have biased interpretations of its role in the Arctic and Baltic ecosystems. According to the results presented in this thesis, the potential predation impact of *M. ovum* was high when assuming relatively homogenous distributions of *M. ovum* and its prey, but it was even higher when patchiness of both predators and prey was taken into account. The potential predation impact was further affected by extensive spatial and seasonal migration patterns. Therefore, to adequately model prey–predator interactions, more emphasis should be placed on the fine-scale distribution patterns of predators and prey. Also, different populations of a single species can have very different trophic roles in the food web due to the great difference in body size, as exemplified in this thesis with two populations of *M. ovum*. In the Arctic, *M. ovum* is a voracious predator of copepods (*Calanus* spp.), while in the Baltic, the substantially smaller *M. ovum* individuals mainly prey upon pico- and microplankton. Thus, generalizing and extrapolating ecological traits such as diet and foraging behavior from one population to another can be misleading. Moreover, the future of the two studied populations of *M. ovum* is likely to differ substantially because their distribution area will be differently affected by climate change; the distribution area is predicted to diminish in the Baltic Sea and remain more or less constant in the Arctic.

To conclude, this thesis demonstrates that our current knowledge on the diversity, role, and potential future changes of the ctenophores in pelagic communities is still very incomplete. Thus, to properly understand the ecological impact of ctenophores at present and in the near future, this thesis suggests that all available techniques need to be applied in species identification, and that clear recommendations for a proper assessment of routine ctenophore monitoring are urgently needed.

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Tiivistelmä:

KAMPAMANEETTIEN MONIMUOTOISUUDESTA JA EKOLOGISESTA ROOLISTA – ESIMERKKINÄ JÄÄ- JA ITÄMEREN *MERTENSIA OVUM*

Hyytelömäisen eläinplanktonin, kuten esimerkiksi kampamaneettien, saama huomio on kasvanut räjähdysmäisesti viimeisen vuosikymmenen aikana. Keskustelua on aiheuttanut lähinnä hyytelöplanktonin mahdollinen maailmanlaajuinen runsastuminen, vaikka tutkijat eivät olekaan tästä yksimielisiä. Kiinnostuksen heräämisestä huolimatta hyytelöplankton on edelleen huonosti tunnettu eläinryhmä. Hyytelöplanktonia ei usein huomioida perinteisissä ravintoverkkotutkimuksissa eikä seurantaohjelmissa, ja sitä pidetäänkin vaikeimmin tutkittavana planktonisena ryhmänä. Näin ollen tieto hyytelöplanktonin monimuotoisuudesta ja ekologisesta roolista on usein joko yksinkertaistettua tai kokonaan väärinymmärrettyä, mikä voi johtaa virheellisiin päätelmiin planktonekosysteemin toiminnasta. Tiedetään kuitenkin, että muun muassa kampamaneetit ovat tehokkaita saalistajia, kykenevät saaliin määrästä riippuen säätelemään kokoaan ja aineenvaihduntaansa, lisääntymään suotuisissa oloissa nopeasti sekä sopeutumaan suuriinkin fysikaalisten tekijöiden, kuten lämpötilan, muutoksiin, minkä vuoksi ne todennäköisesti kykenevät selviytymään voittajina ja jopa runsastumaan tulevaisuuden muuttuvassa ympäristössä.

Arktisella alueella tieto kampamaneeteista pohjautuu muutamaan epäsystemaattiseen ja hajanaiseen runsausarviointiin ja ravinnonkäyttötutkimukseen. Itämerellä eläinplanktontutkimuksessa on käytössä alueen valtioiden yhteinen seurantaohjelma, mutta tästä huolimatta arktisen kampamaneetin, *Mertensia ovum*in, rooli Itämerellä on ollut mysteeri sen jälkeen kun se vuonna 2007 ensimmäisen kerran havaittiin. Tässä väitöskirjatutkimuksessa on tarkasteltu sekä Itämeren että arktisen alueen Cydippida-lahkon kampamaneettien monimuotoisuutta ja merkitystä ravintoketjussa. Tutkimuksen osajulkaisut yhdistelevät laajamittaista, systemaattista näytteenottoa, laboratoriokokeita, lajintunnistusta ja koko ulappayhteisön rakenteen tutkimusta. Osajulkaisuissa arvioidaan Cydippida-lahkon lajirunsautta käyttäen valomikroskopiaa ja uudempia geneettisiä lajintunnistusmenetelmiä sekä tutkitaan *M. ovum*in ravinnonkäyttöä perinteisillä ja molekyylitason menetelmillä. Näiden tutkimusten tavoitteena on ollut selventää tietoa kampamaneettien roolista merten ekosysteemeissä.

Morfologisten ja molekyylitason tunnistusmenetelmien yhdistelmä paljasti, että hallitsevan *Mertensia ovum*in kanssa arktisilla vesillä esiintyvät myös *Euplokamis* sp. ja vielä kuvaamaton Mertensiidae-laji. Samoin *Euplokamis* sp. -laji havaittiin ensimmäisen kerran Itämeren suulla osana laajamittaisempaa amerikankampamaneetin, *Mnemiopsis leidyi*n, ja arktisen kampamaneetin, *Mertensia ovum*in, seurantaa. Laajamittaisista näytteenotoista huolimatta *Pleurobrachia pileus* -lajia, jonka on aiemmin raportoitu esiintyvän yleisesti arktisella alueella ja olevan läsnä koko Itämeren alueella (ja joka on aiemmin raportoitu ainoaksi kampamaneettilajiksi pohjoisella Itämerellä), ei havaittu kummallakaan tutkimusalueella. Väitöskirjatyö osoittaa, että perinteiset morfologiset lajitunnistusmenetelmät eivät yksin riitä. On ilmiselvää, että kampamaneettilajit on yleisesti puutteellisesti kuvattu. Lisäksi julkaistujen geenisekvenssien vähyys rajoittaa tarkkuutta, jolle lajit pystytään geneettisillä tunnistusmenetelmillä luokittelemaan. Geneettinen luokittelu on lähempänä suku- tai heimotasoa kuin oikeaa lajitasoa. Yksi väitöskirjan johtopäätöksistä onkin, että kampamaneettien lajintunnistus on varminta, kun yksilöiden valokuvat yhdistetään morfologisten ja molekyylitason tunnistusmenetelmien kanssa.

Tieto *Mertensia ovum*in roolista arktisen alueen ja Itämeren ekosysteemeissä on ollut vääristynyttä, koska tarkkoja tiheystietoja ja historiallista tutkimustietoa on ollut rajoitetusti. Väitöskirjan kahden viimeisen osa-

julkaisun perusteella on selvää, että *M. ovum*in vaikutus planktonyhteisössä on suurempi kuin on aikaisemmin ajateltu, etenkin jos lajin ja sen saaliiden laikuittainen esiintyminen otetaan huomioon. Myös alueellinen ja ajallinen vaelluskäyttäytyminen vaikuttavat potentiaaliseen saalistustehokkuuteen. Näin ollen saalistajan ja saaliiden laikuittaiseen esiintymiseen olisi kiinnitettävä enemmän huomiota, jotta peto–saalis -vuorovaikutussuhteet saataisiin mallinnettua oikein. Lisäksi saman lajin yhteisöt voivat edustaa eri ravintoverkon tasoja eri alueilla riippuen esimerkiksi yksilöiden kokojakaumasta, kuten arktisen alueen ja Itämeren *M. ovum* -yhteisöt osoittavat. Arktisella alueella *M. ovum* on kyltymätön saalistaja, jonka pääasiallista ravintoa ovat hankajalkaisäyriäiset (*Calanus* spp.). Itämeren yhteisön yksilöt ovat kooltaan huomattavasti pienempiä ja ne syövät lähinnä piko- ja mikroplanktonia. Siten yleistykset lajin ekologisista ominaisuuksista yhteisöstä toiseen voivat olla hyvinkin harhaanjohtavia. Erilaisen ravintokäyttäytymisen lisäksi nämä *M. ovum* -populaatiot kohtaavat tulevaisuuden ympäristömuutokset eri tavoin, sillä ilmastonmuutos vaikuttaa eri tavalla eri levinneisyysalueilla; Itämerellä esiintymisalueen on ennakoitu pienenevän, kun taas arktisella alueella alue tulee pysymään lähes muuttumattomana.

Tämä väitöskirja havainnollistaa, että nykyinen tietomme kampamaneettien monimuotoisuudesta, roolista ulapan ekosysteemissä ja selviytyminen muuttuvassa ympäristössä on edelleen hyvin puutteellista. Väitöskirja myös osoittaa, että voidaksemme ymmärtää kampamaneettien, ja muidenkin hyytelöplanktonryhmien, ekologista roolia ja vaikutusta nyt ja tulevaisuudessa, lajintunnistus olisi tehtävä täsmällisesti asianmukaisia menetelmiä yhdistellen. Erityisen tärkeää olisi suunnitella selkeät suositukset, jotta hyytelöplankton otettaisiin pysyvästi mukaan alueellisiin seurantaohjelmiin.

Sammendrag:

FORSTÅELSE AV RIBBEMANETERS (CTENOPHORA) BIODIVERSITET OG ØKOLOGISKE BETYDNING – LÆRDOM FRA ARKTISK OG BALTISK *MERTENSIA OVUM*

Geléaktige dyreplankton, for eksempel ribbemaneter (Ctenophora), har vakt oppsikt i løpet av det siste tiåret, hovedsakelig på grunn av gåten rundt de potensielt økte forekomstene rundt om i verden. Til tross for den økte oppmerksomheten, er maneter fortsatt en lite kjent gruppe av dyr. De er lite undersøkt eller helt ignorert i de fleste næringsnett-undersøkelser og overvåkingsprogrammer, og er definert som en av de vanskeligste gruppene av pelagiske dyr å studere. Følgelig er deres artssammensetning og økologiske rolle ofte unyansert og misforstått, noe som kan gi et skjevt bilde av marine økosystemers struktur og dynamikk. I tillegg kan ribbemaneter tolerere store endringer i temperatur og saltholdighet, de har et stort vekstpotensiale, reproduserer i hurtig tempo, og kan også tåle lange perioder med matmangel, da de tærer på sin egen kropp og krymper i størrelse. Gunstige vekstbetingelser med rikelig tilgang på planktonføde kan resultere i masseoppblomstringer.

Tidligere forskning på ribbemaneter i Arktis består av sparsomme fødeundersøkelser og biomasseestimater, som mangler en systematisk og uniform tilnærming. I Østersjøen, til tross for regelmessige planktonovervåkingsprogrammer som er utført av de omliggende landene, har rollen til den arktiske ribbemaneten *Mertensia ovum* i dette økosystemet vært ukjent siden den i 2007 ble observert for første gang. I denne avhandlingen ble artssammensetningen og den økologiske rollen til ribbemaneter i orden Cydippida i Svalbards farvann og i Østersjøen studert. Studien kombinerer omfattende, systematisk prøvetaking, laboratorieforsøk, morfologiske (lysmikroskopi) samt nyere genetiske metoder for artsidentifikasjon, og både konvensjonelle og molekylære analyser av diett. Målet med denne studien har vært å øke forståelsen av ribbemaneters rolle i marine økosystemer, spesielt i Arktis og Østersjøen.

En kombinasjon av morfologisk og molekylær artsidentifikasjon viste at ribbemanetene *Euplokamis* sp. og en uidentifisert mertensiid art opptrer sammen med den dominerende *M. ovum* i arktiske farvann. I denne studien ble også den første observasjonen av *Euplokamis* sp. i innløpet til Østersjøen dokumentert i forbindelse med omfattende, systematisk prøvetaking av *Mnemiopsis leidyi* og *M. ovum*. En annen interessant observasjon var at *Pleurobrachia pileus*, sjøstikkelsbær, som tidligere er rapportert til å vanligvis opptre sammen med *M. ovum* i Arktis og være utbredt i hele Østersjøen (og tidligere rapportert som den eneste ribbemanet-arten i den nordlige delen av Østersjøen), ikke ble funnet i noen av studieområdene. Avhandlingen demonstrerer at morfologisk artsidentifikasjon alene ikke er tilstrekkelig. I tillegg mangler mange ribbemanet-arter en nøyaktig beskrivelse, samt publiserte DNA-sekvenser, noe som begrenser identifikasjonen til slekts- eller familienivå. Det bør legges mer vekt på å kombinere morfologiske og molekylære metoder sammen med fotografier for å oppnå solid taksonomisk identifisering og utfyllende artsbeskrivelser.

Mangelen på omfattende, langsiktig kartlegging og nøyaktige estimater av populasjonen av *M. ovum* har påvirket tolkningen av dens rolle i de arktiske og baltiske økosystemer. Ifølge resultatene som presenteres i denne avhandlingen, har *M. ovum* stor påvirkning på økosystemet gjennom predasjon når man antar en relativt homogen distribusjon av *M. ovum* og dens byttedyr. Predasjonseffekten var enda høyere når man antok en heterogen fordeling av både rovdyr og byttedyr, og ble ytterligere påvirket av romlige og temporale vandringsmønstre. For å modellere byttedyr-predatorinteraksjoner på en tilfredsstillende måte bør man legge mer vekt på finskala distribusjon av rovdyr og byttedyr. Dessuten kan ulike populasjoner av en enkelt art har svært ulike trofiske roller i næringsnettet på grunn av den store forskjellen i kroppsstørrelse, noe som

er eksemplifisert med to populasjoner av *M. ovum* i denne avhandlingen. I Arktis er *M. ovum* predator på dyreplankton, særlig på copepoder (*Calanus* spp.), mens i Østersjøen, der individene er betydelig mindre, beiter de hovedsakelig på pico- og mikroplankton. Derfor kan generalisering av økologiske egenskaper, som næringsvalg og predasjonsatferd, fra en populasjon til en annen være misvisende. Videre er fremtiden for de to undersøkte populasjonene av *M. ovum* sannsynligvis vesentlig forskjellig, fordi deres utbredelsesområder vil bli påvirket av klimaendringer på ulike måter; distribusjonsområdet forventes å bli mindre i Østersjøen og å forbli mer eller mindre konstant i Arktis.

For å konkludere, viser denne avhandlingen at vår nåværende kunnskap om ribbemaneters biologiske mangfold, økologiske rolle og mulige fremtidige endringer i pelagiske økosystemer fortsatt er veldig ufullstendig. For å forstå ribbemaneters økologiske påvirkning i dag og i nær fremtid, trenger man alle tilgjengelige teknikker i artsidentifikasjon, og det er et sterkt behov for klare anbefalinger for rutineovervåking av ribbemaneter.

CONTENTS

1. INTRODUCTION AND BACKGROUND

1.1. Gelatinous zooplankton – past and present

Since the mid-1990s, both scientific and general public reports on jellyfish have been increasing (e.g. Condon et al. 2012, Duarte et al 2012, Gibbons & Richardson 2013). Most of these reports address the possible global increase in the gelatinous part of the plankton community, which appears to have been promoted by human-induced stresses and which can potentially alter the structure and functioning of marine ecosystems (e.g. Brodeur et al. 1999, Lynam et al. 2006, Hay 2006, Daskalov et al. 2007, Richardson et al. 2009, Purcell 2012). However, the substantial global increase in gelatinous zooplankton abundance has recently been questioned. While a number of anthropogenic mechanisms capable of promoting increases locally or on larger scales have been recognized, global increase has not been proven (see chapter 1.6, Condon et al. 2012). Still, the rise in interest is evident, as Condon et al. (2012) demonstrated in a search performed on the Web of Science and in Google News using the search terms 'jellyfish', 'gelatinous zooplankton' and 'ctenophore', and as Gibbons and Richardson (2013) indicated when comparing the increase in the peer-reviewed literature on jellyfish to that on copepods.

Regardless of the increase in the number of reports, the diversity of gelatinous zooplankton and their ecology is often exceptionally oversimplified and misunderstood, as jellyfish research is considered to be in its infancy and ctenophores are considered to represent the greatest challenge in oceanographic sampling (e.g. Harbison et al. 1978, Gibbons & Richardson 2013). Even the term 'jellyfish' seems to be an overarching synonym for taxonomically different groups sharing the features of a soft body, transparency, a water content of at least 95 %, and a planktonic lifestyle (e.g. Richardson et al. 2009, Condon et al. 2012, Gibbons & Richardson 2013). This basic oversimplification of similarities makes it easy to lump various groups, such as ctenophores, cnidarians, and pelagic tunicates, together into a single, catch-all category, 'jellyfish', without any taxonomic meaning. In reality, the distinct morphologies and thus ecological roles of the species categorized as 'jellyfish' can yield ecological outcomes as vastly different as, say, lumping lions and gazelles into a single ecological group called Chordata when studying predation on the Serengeti (as discussed in Boero & Mills 1997, Boero et al. 2008, Condon et al. 2012). While the generic term 'jellyfish' usually refers to different groups altogether, this thesis focuses on the identification, distribution, and ecology of one group: the ctenophores.

As the increased interest of the public and the research community shows, it could be said that we are currently living in the 'golden age of gelata' (as discussed in Haddock 2004). While methodologies have developed significantly, the lack of systematic gelatinous zooplankton data and research has been well acknowledged by the jellyfish research community (e.g. Condon et al. 2012, Gibbons & Richardson 2013, Fourth International Jellyfish Bloom Symposium 2013). Although we appear to be in an ideal time for dramatically expanding our understanding of gelatinous zooplankton, there are severe obstacles to cross and uncertainties to recognize, even

among a single taxonomic group of jellyfish, the cydippid ctenophores.

1.2. The challenges of ctenophore species identification

The marine zooplankton is taxonomically diverse, comprising more than 7,000 species in 15 phyla (Boltovskoy et al. 2002). It is also taxonomically challenging as it requires considerable time and effort to routinely identify and characterize its diversity (May 1988, Colwell & Coddington 1994, Bucklin, Hopcroft et al. 2010, Bucklin, Nishida et al. 2010). Ctenophores are no different. Ctenophores are an understudied group of organisms with approximately 100 to 250 species described globally (e.g. Haddock 2004, Mills & Haddock 2007, Richardson et al. 2009, Mills 2013). The estimated number of species in the group varies considerably depending on the source and whether potential synonymies have been taken into consideration. Only 100 to 150 are thought to be actual species (Mills & Haddock 2007). In addition, the scientific community acknowledges that the number of ctenophore species has been underestimated globally – at least 25 to 50 species have not yet been formally described (Mills & Haddock 2007, Mianzan et al. 2009, Mills 2013), and the number of undescribed ctenophore species in the deep-sea regions has not even been estimated (Podar et al. 2001, Mills & Haddock 2007).

Ecological research usually requires rapid and accurate identification, but the researchers conducting the work may not have the taxonomic knowledge to do so with the necessary precision and consistency. While it may appear simple to count the species number of a sample, identifying specimens to the species level is time consuming and requires special taxonomic expertise. Moreover, morphological species identification has three significant limitations. First, although modern interactive versions of the traditional dichotomous taxonomic identification keys used today represent a major advance, they require such advanced skills for accurate use that misidentifications are common (Hebert et al. 2010). Even though ctenophores are morphologically diverse, they possess a number of derived characters (synapomorphies), such as biradial symmetry, eight rows of combs or ctenes controlled by an apical organ, and specialized adhesive cells (e.g. Harbison 1985, Podar et al. 2001, McConville 2011). This relative scarcity of available species specific features makes constructing good keys difficult and hampers correct identification. Second, morphological keys are often made for a particular life stage or gender, and many individuals cannot therefore be identified (Harbison & Madin 1982). For example, all ctenophores except the beroids have a 'cydippid' larval stage, which is similar to small-sized, cydippid adult specimens (Mayer 1912, Hyman 1940, Harbison & Madin 1982, Harbison 1985, Podar et al. 2001, Gorokhova & Lehtiniemi 2010). Finally, in ecological samples, the extremely fragile specimens are often damaged when collected with traditional sampling nets or preserved with conventional fixatives, leaving researchers with unidentifiable bits and pieces (Podar et al. 2001, Thibault-Botha & Bowen 2003, Mills & Haddock 2007, Gorokhova & Lehtiniemi 2010, Raskoff et al. 2010). Thus, the order or family of ctenophores can usually be identified but assignment to the species level is more demanding when only using traditional morphological identification procedures (e.g. McConville 2011).

The problems of morphology-based identification, and the declining pool of taxonomists, are clear indicators of a demand for a new approach to species recognition. Various molecular methods have been developed, including DNA hybridization (Britten & Kohne 1968), species-specific PCR (e.g. Gorokhova et al. 2009), random amplified polymorphic DNA (Williams et al. 1990), restriction fragment length polymorphisms (Saiki et al. 1985), single strand conformational polymorphic DNA (Orita et al. 1989), and sequencing of PCR products (e.g. Podar et al. 2001), each with their advantages and disadvantages. DNA-based species identification methods have made it possible to rapidly and inexpensively identify field-collected planktonic organisms, and at best can convey the ability to obtain good information even from damaged pieces of specimens.

DNA barcoding, the use of short sequences of one or few genes (mostly mitochondrial DNA [mtDNA COI]), has undoubtedly been the most commonly used molecular method for identifying plankton (e.g. Webb et al. 2006, Bucklin et al. 2007, Ortman et al. 2010, CMarZ 2013). Barcoding has also been used for population genetic and phylogeographic analysis, gut content analysis, seafood safety, delimiting species boundaries, the detection of invasive species, revealing cryptic species, and discovering new species (e.g. Dawson & Jakobs 2001, Dawson & Martin 2001, Ortman et al. 2010, Bucklin, Nishida et al. 2010, Bucklin et al. 2011). However, concerns have been raised over the adoption of barcoding, with some studies suggesting it would be a step backwards (Mallet and Willmott 2003, Seberg et al. 2003, Lipscomb et al. 2003, Meyer & Paulay 2005). Opponents note that (mtDNA) sequences alone may be insufficient to accurately identify species, due to genetic differentiation which does not necessarily track species boundaries (Avise 2004). For example, Funk & Omland (2003) found that approx. 23 % of surveyed metazoan species are genetically polyphyletic or paraphyletic, implying that they would not be differentiable by barcoding techniques. In addition, this method has not been as easily applied to gelatinous zooplankton as it has to some other groups (Ortman 2008, Sundberg et al 2009, Bucklin et al. 2011), and it has rarely been successfully used for ctenophores (Bucklin et al. 2011, S. Laakmann, pers. comm. 6/2012, BOLD Systems 2013).

The small subunit (18S) ribosomal RNA gene has been shown to be a useful marker, allowing phylogenetic reconstruction and organism recognition at various taxonomic levels in some eukaryotes (e.g. Zimmermann et al. 2011), but not in all (Pawlowski et al. 2012). Unfortunately, ctenophores are at risk of falling into the latter category. The only analysis conducted with the 18S rDNA genes from more than 20 ctenophore species revealed a highly conserved length and limited sequence divergence within the phylum (Podar et al. 2001). No other major metazoan phylum is known to have such conserved ribosomal RNA genes. However, as an alternative, the more variable ITS regions have been used independently or included in analyses, allowing more comprehensive phylogenetic analysis. In species recognition, this region has been shown to be useful among a variety of organisms (Anderson & Adlard 1994, Dawson & Jacobs 2001, Schroth et al. 2002). The ITS region has been used several times to identify ctenophores (Podar et al. 2001, Bayha et al. 2004, Gorokhova et al. 2009) and it appears to be easily amplified within this phylum.

The major problem with the solely molecular species identification approach is that much of the sequence data in the databases are from isolates that were incorrectly identified or named. The use of these database sequences to identify species by sequence similarity perpetuates the problem of wrong species identification (Ko Ko et al. 2011). The prospect of assigning an unknown species to a known is promising for well-known, systematically sampled groups that have been comprehensively studied by genetic and morphological taxonomy, but less effective for taxa such as ctenophores, where taxonomic examination has not been thorough, and species recognition is limited to a few traditional character sets (e.g. Meyer & Paulay 2005).

Therefore, careful taxonomic revision of well photographically documented specimens together with simple and standardized molecular methods must be used to differentiate between morphologically similar ctenophore species and life stages. This is crucial for field surveys and monitoring programs because ctenophores are often collected by scientists unfamiliar with these unique taxa (**I–III**, **Thesis summary**).

1.3. Misleading ctenophore abundance data

Long time series are essential for observing species distributions and abundances, and are therefore one of the core requirements for a wide variety of ecosystem studies. These systematic and continuous environmental records are also vital for detecting changes in marine ecosystems over seasonal, interannual, decadal and even longer time frames (e.g. Condon et al. 2012). These changes may be uninterrupted, or they may occur as sudden shifts, requiring long time series for better detection of trends and statistical comparison. Every year of data added to a time series makes the entire dataset more valuable than it was the year before (see e.g. Brodeur et al. 2002, 2008). These data sets are also the basis for ecological models that can predict ecosystem dynamics under changing environmental conditions (Niiranen et al. 2012) which are in demand due to the challenge of climate change in combination with the growing need for marine resources (Tomczak et al. 2012).

For a long time, gelatinous zooplankton were considered as unimportant, both ecologically (as dead-ends of the food web in marine ecosystems) and commercially. During oceanographic surveys, it was more common to find the answer to the questions ‘how many?’ and ‘how much?’ before having answered to the question ‘who?’, which led the small torn pieces of gelatinous material to be unidentified and uncounted. It also appears that if an organism could not be fixed with conventional preservatives, it was considered as unimportant (e.g. Haddock 2004). Recently, as their importance has been more widely acknowledged, there has been considerable interest in gelatinous species (e.g. Bucklin, Nishida et al. 2010, Bazooca 2013, Condon et al. 2013). However, there have been problems when gathering extensive, continuous long-term datasets. Datasets have been biased towards certain seasons, commercially exploited areas and economically important species. In addition, methodology used is often selective towards certain species and life stages, and predicts homogeneity of oceanographic conditions and even distribution of plankton communities over a wide range of localities (e.g. Magurran et al 2010, Condon et al.

2012). Thus, in contrast to commercial fish species and other zooplankton taxa, the abundance of ctenophores has not been monitored on a regular basis (e.g. Condon et al. 2012), and they have been completely excluded as a functional group from current ecological models (e.g. Tomczak et al. 2012).

As oceans are highly divergent and patchiness is pronounced, the process of formulating models for marine populations involves averaging spatial heterogeneities in some way (Pitchford & Brindley 2001). Patchiness in marine zooplankton populations is common and exhibited over a continuum of scales (e.g. Dagg 1977, Omori & Hamner 1982, Davis et al. 1992), and it appears to be particularly pronounced among ctenophores (e.g. Omori & Hamner 1982, Arai 1992, Graham et al. 2001). Furthermore, many ctenophore species respond to favorable conditions by rapid population increase, making interpretation of population estimates from monitoring programs extremely difficult (Boero et al. 2008, Richardson & Gibbons 2008). Also, the nets commonly used in zooplankton sampling and monitoring programs are too small in area (approx. 0.25 m^2) to reliably estimate dispersed taxa such as ctenophores. These plankton nets may either pass through a number of discrete aggregations or miss these aggregations altogether, and thus greatly underestimate their diversity and abundance (e.g. Naumov 1960, 1961, Ospovat 1985, Harbison 1986, Harbison et al. 1978, Stepanjants 1989, Raskoff et al. 2003, 2005, Purcell 2009). However, the aggregations have become a great concern, as the number of reports on the intensity and frequency of gelatinous blooms has increased worldwide (e.g. Richardson et al. 2009, Condon et al. 2012).

Therefore, reliable data on ctenophore distribution and abundance, including small-scale spatial and temporal resolution, and analysis of their population dynamics are required to properly understand the impact of ctenophores within ecosystems (**II**, **IV**, **Thesis summary**).

1.4. The indeterminate role of ctenophores

Despite the fact that the importance of gelatinous zooplankton in marine food webs has been recognized, ecological knowledge of gelatinous zooplankton is strongly biased towards particular species, mainly scyphozoan medusae and the ctenophore *Mnemiopsis leidyi* (e.g. Pang & Martindale 2009, Augustine et al. 2013, Fourth International Jellyfish Bloom Symposium 2013). Being more robust, they are more suitable for *in situ* studies and laboratory experiments. Out of necessity, ecosystem modeling efforts tend to emphasize only the elements directly known to link key species in the ecosystem, while species among the ctenophores that are difficult to detect, quantify, identify, and study experimentally are often ignored (e.g. Raskoff et al. 2003, Pauly et al. 2009, Gibbons & Richardson 2013). This can lead to biased views of ecosystem functioning.

It is well known that high rates of feeding, growth, and reproduction enable the ctenophores to rapidly reach high abundances (Purcell & Arai 2001). Hence, ctenophore blooms may have distinct consequences for planktonic food web structure and ecosystem function through top-down and bottom-up effects (e.g. Condon et al. 2010, Dinasquet et al. 2012). For instance, gelatinous zooplankton predation

may regulate the zooplankton biomass, and thus structure the planktonic food web as a whole (Stibor et al. 2004, Turk et al. 2008). Also, some species have been reported to stimulate bacterioplankton growth by direct release of nutrients from tissue, mucus secretion, excretion, and also by sloppy feeding (Nemazie et al. 1993, Riemann et al. 2006, Titelman et al. 2006, Pitt et al. 2009, Condon et al. 2011). Furthermore, it is likely that the link between gelatinous zooplankton and bacteria results in an alternative carbon pathway for resource-specific bacterioplankton, directing carbon away from higher trophic levels. Thus, major shifts in microbial structure and function associated with jellyfish blooms in coastal and estuarine systems may arise (the jelly-carbon shunt; Condon et al. 2011).

Ctenophores are known to be voracious predators, feeding primarily on zooplankton such as copepods (e.g. Smith & Schnack-Schiel 1990, Conover & Huntley1991, Mumm et al. 1998). Despite the reported high predatory impact of some ctenophore species, such as *Mnemiopsis leidyi* (e.g. Shiganova & Bulgakova 2000, Shiganova et al. 2004, Colin et al. 2010), very little is known about the specifics of predator–prey encounter events, since they cannot usually be observed *in situ* (but see Madin 1988, Haddock 2007). Currently, most predation impact studies and many of the most commonly used predator–prey models assume that populations are homogeneously distributed in space (e.g. Murdoch 1973). As patchiness seems to be particularly distinct among ctenophores (e.g. Omori & Hamner 1982, Graham et al. 2001), ignoring spatial patterns can lead to erroneous conclusions concerning their predation impact.

In addition, the relationship between predator size and prey size is of great importance when determining the outcome of interactions among species (Scharf et al. 2000). Thus, direct extrapolation from one species, or population, to another raises uncertainties when modeling basic ecological traits such as diet and foraging behavior, especially if individual sizes of the predators clearly differ between the populations. From studies on *Mnemiopsis leidyi*, it is known that feeding mechanisms and prey preferences change during ontogeny. While newly hatched tentaculate larvae capture nano- or microplankton such as flagellates and ciliates on their tentacles (Sullivan & Gifford 2004, 2007), larger tentaculate or transitional stage larvae can also feed on large prey such as mesozooplankton (Stanlaw et al. 1981). However, knowledge from other ctenophore species is currently lacking, particularly in relation to predation impacts at lower trophic levels.

1.5. Ctenophores in the Arctic Ocean and Baltic Sea

Existing ctenophore studies are not only biased towards *Mnemiopsis leidyi* (Augustine et al. 2013), but also towards tropical and temperate waters. Due to its low accessibility, the Arctic is the least studied among the major oceans on Earth. The taxonomic composition and life-history strategies of the crustaceans in the Arctic are moderately well known (Smith & Schnack-Schiel 1990, Mumm et al. 1998, Deibel & Daly 2007), whereas the abundance, composition, and ecology of ctenophores are not (e.g. Ospovat 1985, Swanberg 1974, Swanberg & Båmstedt 1991a, b, Raskoff et al. 2005, 2010). Three species of ctenophores have been recorded from the coastal Svalbard area: *Mertensia ovum*

(Cydippida, Fabricius 1780), *Pleurobrachia pileus* (Cydippida, Müller 1776), and *Beroe cucumis* (Beroidea, Fabricius 1780) (Palerud et al. 2004). In addition, *Dryodora glandiformis* (Cydippida, Mertens 1833), *Beroa abyssicola* (Beroidea, Mortensen 1927) and *Bolinopsis infundibulum* (Lobata, Müller 1776) have been reported to occur in the Barents Sea region (e.g. Sirenko 2001). Despite the recent establishment of the Arctic Marine Biodiversity Monitoring Plan supported by Conservation of Arctic Flora and Fauna (CAFF 2013), the data on these taxa consist of several abundance estimates and dietary studies lacking a systematic or integrative approach (e.g. Falk-Petersen et al. 2002, Søreide et al. 2003, Lundberg et al. 2006, Walkusz et al. 2009).

In the Baltic Sea, a well-established routine plankton monitoring program is conducted by the surrounding nations through the Helsinki Commission (HELCOM). Despite the extensiveness of the program, the ctenophore community has only been comprehensively assessed during the last six years, since the first appearance of *Mnemiopsis leidyi* (Lobata, Agassiz 1865) (e.g. Hansson 2006). Reports of *M. leidyi* occurring in the northern and central Baltic Sea, including the Gulf of Bothnia and Finland (Lehtiniemi et al. 2007, Viitasalo et al. 2008), turned out to be a misidentification, and the species was later confirmed to be a previously unreported species, *Mertensia ovum* (Gorokhova et al. 2009, Gorokhova & Lehtiniemi 2010). Before the appearance of *M. ovum*, *Pleurobrachia pileus* was the only ctenophore known to be present almost throughout the Baltic Sea (e.g. Mielck 1926, Ackefors 1969, Vuorinen 1987), whereas *Bolinopsis infundibulum* (Lobata, Müller 1776), *Beroe cucumis*, *B. gracilis* (Beroidea, Künne 1939), and *M. leidyi* have been recorded in the southern and western parts (e.g. Javidpour et al. 2006, Haslob et al. 2007, Huwer et al. 2008, Jaspers et al. 2013, Haraldsson 2013). Similarly to the Arctic, data on these taxa consist of several abundance estimates and dietary studies lacking a systematic or integrative approach (e.g. Lehtiniemi et al. 2007, Viitasalo et al. 2008, Jaspers et al. 2012). In addition, since its first reported appearance in the Baltic Sea in 2009, the role of *M. ovum* in this ecosystem has been undefined. The Baltic Sea population of *M. ovum* is interesting because there are no records of this species in other low salinity environments, or of its trophic role in brackish waters.

1.6. Why should we care? Gelatinous zooplankton tomorrow

Although gelatinous zooplankton aggregations are known to be a natural phenomenon even in healthy pelagic ecosystems (Graham et al. 2001, Hamner & Dawson 2009, Condon et al. 2012), various possible anthropogenic drivers, acting both separately and synergistically, have been suggested for their apparent increase: the depletion of predators and competitors by overfishing, accidental translocations, eutrophication, changes in freshwater flows, human modifications of coastal geomorphology, changes in optical conditions and climate change (Mills 2001, Purcell et al. 2007, Purcell 2012). Nevertheless, without knowledge of ecosystem baselines, it is very difficult to determine whether the intensity and magnitude of blooms has increased (e.g. Richardson et al. 2009, Kogovšek et al. 2010), or whether they are fluctuating with climatic cycles (Brodeur et al. 2002, 2008, Purcell et al. 2007, Condon et al. 2012, 2013).

It is evident that the oceans are undergoing changes at an unprecedented rate, especially at high latitudes (e.g. Meier et al. 2006, BACC author team 2008, Wassmann et al. 2011, Meier, Andersson et al. 2012, Meier, Müller-Karulis et al. 2012). These changes are predicted to result in large and widespread alterations in the marine ecosystems, their species richness, community structure and functioning (Purcell et al. 2010, Søreide et al. 2010, Narayanaswami et al 2010, Doney et al. 2012). Simultaneously, shipping activity is increasing, particularly in the Arctic due to the opening of the north-east passage, potentially triggering changes in the biodiversity (e.g. Stachowicz et al. 2002, Molnar et al. 2008). At the same time, gelatinous zooplankton, such as *Mnemiopsis leidyi*, have been reported to be among the worst marine invasive species (Lowe et al. 2000), and share characteristics making them likely to benefit from the changing environmental conditions (Richardson & Gibbons 2008, Richardson et al. 2009, Doney et al. 2012). The ability to tolerate a broad set of environmental and anthropogenic stressors such as low oxygen concentrations (Mills 1984, Condon et al. 2001, Decker et al. 2004, Rutherford & Thuesen 2005), low food conditions (Hamner & Jenssen 1974, 33, Anninsky et al. 2005), and increased temperatures (e.g. Purcell 2005, Purcell et al. 2007, Richardson & Gibbons 2008) might give them an advantage compared to other zooplankton groups (Richardson et al. 2009).

Therefore, the limitations of our current understanding of ctenophores in light of predicted climate change call for a rigorous taxonomic and ecological study of ctenophores to assess ctenophore species distribution, ecological impacts, and potential future changes, as well as for systematic research and monitoring efforts at ecosystem-relevant scales.

2. OUTLINE AND AIMS OF THE THESIS

The overarching aims of this thesis are to:

– provide a comprehensive overview of the biodiversity of cydippid ctenophores in Svalbard waters and in the Baltic Sea;
– provide a basic understanding of the biodiversity and ecological importance of ctenophores in the pelagic communities; and
– elucidate the uncertainties and limitations of our current understanding of ctenophores.

In order to achieve this, the specific issues of species identification, abundance, and role in the food web have been addressed in five complementary studies and with additional data (see Fig. 1, **I–V**, **Thesis summary**).

The species in focus is the common Arctic comb jelly, *Mertensia ovum*, which has been reported to be endemic in the High Arctic and was recently reported for the first time, potentially as an ice-age relict, in the Baltic Sea. In this thesis, extensive *in situ* sampling, morphological and molecular identification analysis, traditional and molecular gut content analysis, manipulative laboratory experiments, as well as several indirect and direct measures of the ctenophores and the pelagic communities they inhabit have been combined. The thesis not only addresses system-specific knowledge gaps, but provides an increased understanding of how important a role the ctenophores might play in the marine ecosystem, as well as suggestions for future studies.

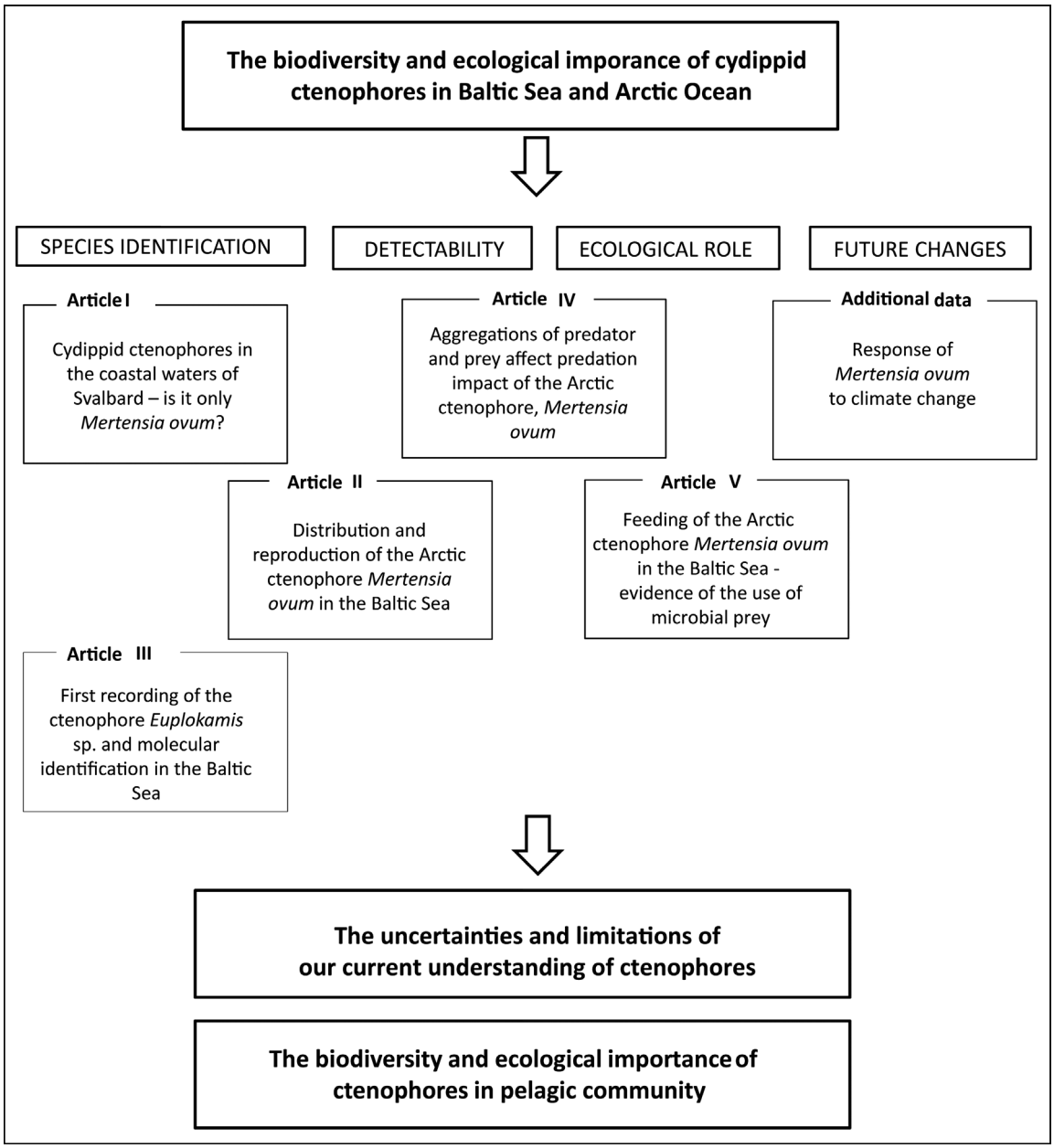


Fig. 1. Conceptual diagram showing how articles I–V build upon each other and contribute to the central theme of the thesis: "*understanding the biodiversity and ecological importance of ctenophores in pelagic communities*" as a whole. Articles I to III investigated species identification, while articles II and IV reveal the uncertainties in the estimation of the abundance of gelatinous zooplankton. Article IV links ctenophore abundance to their role in the ecosystem. Similarly, article V investigates how patterns of basic ecological traits such as feeding are impossible to generalize from one population to another, even within the same species. In addition, the thesis summary looks into the survival potential of *M. ovum* in two different locations with the uncertain aspects of future changes in the climate.

2.1. Detailed aims

*2.1.1. Cydippid ctenophore species identification (**I–III**)*

As discussed above, proper taxonomic identification is fundamental when assessing biodiversity, describing changes in species composition and distribution, or estimating the potential for future changes. Ctenophore identification has severe challenges and limitations, as addressed above. Thus, studies **I–III** focused on cydippid ctenophore species identification with the following study questions:

A) Is the Arctic ctenophore, *Mertensia ovum,* the only cydippid ctenophore occurring in Svalbard waters? (**I**)

B) Does *M. ovum* co-occur with other cydippid ctenophores, such as *Pleurobrachia pileus,* in the Baltic Sea? (**II–III**)

2.1.2. Mertensia ovum *abundance (**II, IV**)*

Reliable data on ctenophore occurrences and abundances are rare, and analysis of their population dynamics is challenging. Studies **II** and **IV** investigated the distribution, seasonality and patchiness of the *M. ovum* populations in the High Arctic and Baltic Sea waters with the following study questions:

C) What is the distribution and abundance of *M. ovum* in the Baltic Sea? (**II**)

D) Can the patchy distribution of *M. ovum* in the Arctic be detected? (**IV**)

2.1.3. Mertensia ovum *as a predator and a grazer (**IV, V**)*

Although most ctenophores are known as voracious predators, our knowledge of their role in the Arctic pelagic food web is very limited. As patchiness in marine zooplankton populations is common, its effects on ecological interactions need to be quantified. Moreover, the great variation in size among *M. ovum* specimens makes extrapolations of their role in the plankton community from the more studied populations inhabiting the Arctic Ocean to the Baltic Sea populations uncertain. Thus, the common belief that most ctenophores, including *M. ovum* in the Arctic, are principally insatiable consumers of mesozooplankton can be misleading in the Baltic Sea. Consequently, the study questions here were:

E) How do the aggregations of predators and preys affect the predation impact? (**IV**)

F) What is the role of *M. ovum* in the Baltic Sea? (**V**)

2.1.4. Response of Mertensia ovum *to climate change (**Thesis summary**)*

Even though the increase in gelatinous zooplankton blooms has recently been questioned due to the lack of long-term data, the general impression is that ctenophores would benefit from climate change. Thus, the effect of future changes in the climate on one gelatinous species, *M. ovum*, in two different populations, the Arctic and Baltic Sea, was examined based on some additional data presented in the thesis summary with the following specific study questions:

G) What are the salinity and temperature limitations within one species, *M. ovum*, and its two distinct populations, and what are the potential effects of climate change? (**Thesis summary**)

3. MATERIAL AND METHODS

3.1. Study sites

The Arctic Ocean can be considered either as a one large ecosystem or as multiple smaller areas each with its own unique characteristics and functions. All the studies in this thesis that were carried out in the Arctic Ocean were conducted in the European side of the Arctic, in Svalbard waters (Fig. 1A, **I**, **IV**, **Thesis summary**). The main characteristics of this area are introduced in detail in Box 1.

All the studies in this thesis that were carried out in the Baltic Sea were mainly conducted in the northern parts of the Baltic Sea: the Gulf of Finland, Archipelago Sea, and Bothnian Bay (Fig. 1B, **II**, **V**, **Thesis summary**). Additional sampling included the southern Baltic Sea and Baltic Proper (**II**), and adjacent waters off the southern Swedish coast (**III**). The main characteristics of these areas are introduced in detail in Box 2.

3.2. General methodology

*3.2.1. Sampling of ctenophores (**I–V, Thesis summary**)*

In 2008–2011, ctenophores in the Arctic were collected during several research cruises on board R/V Jan Mayen (recently renamed RV 'Helmer Hanssen'), R/V Lance and R/V Viking Explorer, and with a small boat (Zodiac) in the area of the Svalbard Archipelago (Fig. 2A) (**I**, **IV**, **Thesis summary**). Ctenophores were collected from the zooplankton samples taken with a multiple plankton sampler (MPS, Hydrobios, Kiel, equipped with 5 closing nets, mesh size 180 μm, opening 0.25 m^2 with a filtering cod end, 0.5 m s^{-1} towing speed), a WP-2 closing net (Hydrobios, Kiel, mesh size 180 μm, opening 0.25 m^2 with a filtering cod end, 0.5 m s^{-1} towing speed), a MIK net (mesh size 1.5 mm, opening 3.15 m^2 with a filtering cod end, 0.5 m s^{-1} towing speed), or a plastic bucket (1-3 l) from surface waters while scuba diving or from a Zodiac.

In 2007–2012, ctenophores were collected on various monitoring (HELCOM) and research cruises on board R/V Aranda, R/V Muikku, R/V Salme, R/V DANA, and R/V ALKOR in the Baltic Sea, from the Baltic Proper to the Gulf of Finland (Fig. 2B). Ctenophores were collected with a WP-2 closing net (Hydrobios, Kiel, mesh size 90–500 μm, opening 0.25 m^2 with a filtering cod end, 0.5 m s^{-1} towing speed) (**V**), a multiple plankton sampler (MPS, Hydrobios, Kiel, equipped with 5 closing nets, mesh size 50 μm, opening 0.25 m^2 with a filtering cod end, 0.5 m s^{-1} towing speed), and a Juday net (mouth area 0.1 m^2 and mesh size 100 μm, 0.5 m s^{-1} towing speed) (**II**).

In addition, ctenophore sampling was conducted in the Gullmar fjord on the west coast of Sweden in 2011 onboard R/V Skagerak (see detailed map in Fig. 1 of study **III**). Sampling was conducted with a WP-3 net (Hydrobios, Kiel, mesh size 450 μm, opening 1 m^2 with a filtering cod end), a multiple plankton sampler (MPS, Hydrobios, Kiel, equipped with 5 closing nets, mesh size 180 μm, opening 0.25 m^2 with a filtering cod end), and with beakers from the surface waters as a part of a routine jellyfish/zooplankton monitoring program (Bazooca 2013).

Immediately after collection, the ctenophores were gently sorted from the other plankton, counted, and measured (oral–aboral length; from oral- to anal opening not including the keels, Fig. 3C, used throughout the study) alive onboard

Box 1. Characteristics of the High Arctic waters

Perhaps the most conspicuous feature that influences different aspects of the Arctic, from taxonomic composition to functional dynamics, is the strong seasonality (Falk-Petersen et al. 2000). The zooplankton community in the area undergoes a change from high densities in late summer and autumn to low abundance in winter and spring (Hassel 1986, Weslawski et al. 1988, Falk-Petersen et al. 1990). Similarly, some of the species undergo a change from high densities in the upper water layers during the summer to seasonal migration to greater depths for overwintering (Falk-Petersen et al. 2008, Walkusz et al. 2009). In addition, part of the plankton community has been reported to perform distinct diel vertical migration (DVM), as the plankton descend to deeper depths during the local midday and move closer to the surface during the local midnight (e.g. Cottier et al. 2006, Falk-Petersen et al. 2008).

The Svalbard archipelago is located on the southern fringe of the European Arctic Ocean (Fig. 2). This region has a complex hydrography, and is influenced by two interconnected current systems: the Atlantic system, with the North Cape Current (NCC) and the West Spitsbergen Current (WSC) as the northern extensions of the Gulf Stream System (GSS), and the Arctic system with the South Cape Current (SCC). The relatively warm and ($T > 3$ ˚C) and saline ($S > 34.9$) Atlantic water mass flows from the south before it turns to the east along the shelf slope north of Svalbard (Saloranta & Svendsen 2001). The cold ($T < 0$ ˚C) and less saline (S 24.3–34.8) Arctic water mass flows from the Barents Sea towards the southern parts of Spitsbergen (Ingvaldsen & Loeng 2009). These two water masses mix and form Transformed Atlantic Water (TAtW) when waters from the WSC penetrate the Spitsbergen continental shelf. TAtW is often slightly colder ($T > 1$ ˚C) and less saline ($S > 34.7$) than Atlantic Water (Gulliksen & Svensen 2004). In addition, several local and seasonal processes in the fjords form local water masses (Ingvaldsen & Loeng 2009), such as the locally formed Winter Cooled Water (WCW), which has a low temperature ($T < -0.5$ °C) and high salinity ($S > 34.4$) (Gulliksen & Svensen 2004). Other locally formed water masses include Local Water (LW) produced by the surface cooling at the end of the Arctic summer, and Surface Water (SW) formed by the glacial melt water in late spring and summer (Gulliksen & Svensen 2004).

In this thesis, the main focus is on three locations around the Svalbard archipelago: Kongsfjord, Rijpfjord, and Billefjord (Fig. 2A). In Kongsfjord, water is periodically influenced by strong Atlantic water intrusion from the WSC, and no ice cover has formed in recent winters (Cottier et al. 2006). In contrast, Rijpfjord is principally characterized by Arctic water and is ice-covered for 6 to 8 months each year (e.g. Ambrose et al. 2012). Billefjord, a side branch of Isfjord, is also seasonally ice-covered (~5 mo of the year). In Billefjord, there is a sill at the entrance that restricts the exchange of water masses, allowing the cold, dense Winter Cooled Water to form and remain in the fjord basin (Walkusz et al. 2009). Each of these fjords has its own mixture of water masses in different depth layers and seasons; thus, the plankton populations of each have distinct abundances and dynamics.

In recent years, the effects of climate change have been especially pronounced in the Atlantic sector of the Arctic (e.g. Karnovsky et al. 2010). The sea ice has declined in extent and thickness as the area has experienced large increases in temperature (Blindheim et al. 2000, Vinje 2001). These changes have primarily been driven by increased advection of the warm and saline Atlantic water (Aagaard et al. 1987, Walczowski & Piechura 2006). It has been predicted that these changes could alter the species compositions by replacing the lipid-rich key Arctic grazers with temperate and less lipid-rich organisms, and thus reduce the current primary production regime, which would have direct negative impacts on higher trophic levels (Falk-Petersen et al. 2007, Steen et al. 2007, Søreide et al. 2010). Furthermore, the increasing shipping activity in the area is expected to trigger changes in the species composition, as a better invasive competitor might exclude others in competitive colonization (Molnar et al. 2008).

Box 2. Characteristics of the Baltic Sea

The Baltic Sea is one of the world's largest brackish water bodies and it is almost completely surrounded by land; only the narrow Danish Straits makes a connection with saline seas (Fig. 2). The combination of relatively high salinity water entering to the Baltic Sea and the large inflow of freshwater from more than 200 rivers creates a unique south–north salinity gradient: from high salinity areas such as 25–30 in the south, and 8–19 in middle, to a stable declining salinity gradient spanning 10–1 towards the eastern and northern ends of the Gulf of Finland and the Bothnian Bay (Fig. 2B, Leppäranta & Myrberg 2009). As the inflowing saline water is denser than the brackish water, the Baltic Sea is stratified with a halocline; the most saline water is found in the deepest parts of the sea.

In this brackish water environment, the salinity is the most crucial factor determining the distribution range and size of most of its inhabitants. Both marine and freshwater species experience difficulties when faced with the brackish water of the Baltic Sea, the salinity being either too low or too high. As a consequence of the large osmotic stress for the organisms, "dwarfism", a severe reduction in the size of a variety of marine species in the low salinity areas, has been noted (e.g. Kautsky & Kautsky 2000).

A similar north–south gradient is also present in the temperature range: water becomes warmer when moving towards the south. During the summer, the Baltic Sea is always temperature stratified (Leppäranta & Myrberg 2009). A thermocline, a layer where the water temperature drops rapidly, normally forms at a depth of 10–30 meters. The thermocline prevents the exchange of water between the upper warm-water layer, which is susceptible to wind mixing, and the lower cold-water layer, where no mixing occurs. In the winter, the upper layer is affected by mixing with the lower layer and by the interaction with the ice cover. The probability and duration of ice cover increases towards the northern and eastern parts of the sea. During normal winters, the ice cover lasts 4–6 months in the Bothnian Bay and 2–4 months in the Gulf of Finland, whereas in the Baltic Proper it lasts less than a month. Only exceptionally cold winters can cause the entire Baltic to freeze over (Leppäranta & Myrberg 2009).

Unlike most other seas and oceans, the Baltic Sea is located entirely on one continental plate instead of lying on a continental divide, which explains why the sea is so shallow compared to other seas. The average depth of the Baltic Sea is only 60 meters, the deepest part being the Landsort Deep in the Baltic Proper (max 459 meters). The deep areas below the halocline in the Baltic Proper often run out of oxygen, and hydrogen sulfide thus forms at the bottom, influencing the communities that live there (Fonselius &Valderrama 2003).

Historically, the Baltic Sea is very young; 12,000 years ago, large parts of the Baltic Sea were still covered by the continental ice sheet of the last glaciation. Since the last ice age, the Baltic Sea basin has gone through several phases of changing shape and salinity (Tikkanen & Oksanen 2002). The current morphological and physico-chemical conditions have developed during the last 8,000 years. There have been phases of higher salinity than at present; thus, only a few true brackish water species have been able to evolve (Pereyra et al. 2009). Likewise, the marine species have not had sufficient time to adapt to the lower salinities. On the other hand, the glacial history has left behind species that originated from the Arctic Ocean and have lived as relicts in glacial lakes formed during the ice age, such as *Monoporeia affinis*, *Pontoporeia femorata*, *Saduria entomon*, and *Mysis relicta* (Segerstråle 1962). Some of the species that are now common in the Baltic Sea, such as the barnacle *Balanus improvisus* and the bivalve *Mya arenaria*, are relative newcomers, having arrived in the Baltic within the last few centuries (Leppäkoski & Olenin 2000). Altogether, approximately 120 invasive species are now present in the Baltic Sea (Baltic Sea Alien Species Database 2013), and other new species are bound to follow in the future. Moreover, based on the regional climate change modeling results, impacts on the marine ecosystem are projected to include increased water temperatures, reduced sea ice cover, and reduced salinity (e.g. Meier et al. 2006, BACC author team 2008, Meier, Andersson et al. 2012, Meier, Müller-Karulis et al. 2012).

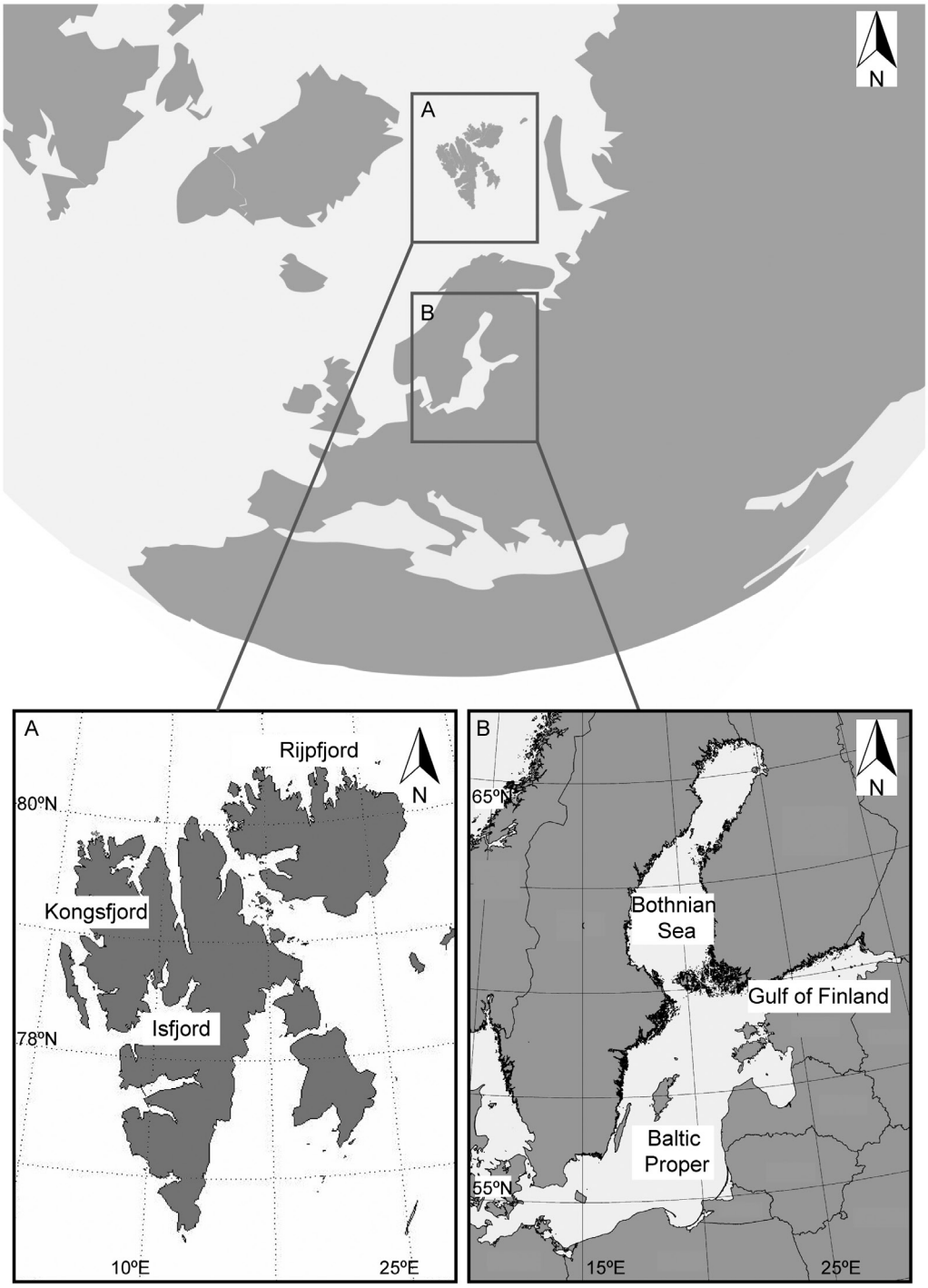


Fig. 2. The main study sites in the Arctic (A) and in the Baltic Sea (B).

the respective research vessels using a dissecting microscope. The ctenophores collected within the HELCOM zooplankton monitoring were preserved in formalin and counted within a year of collection under a dissecting microscope. A set of samples were used to compare the abundances estimated from live and preserved samples. Counts were conducted first from live material and later from the same samples after preservation in 4 % borax-buffered formalin and 4–5 months of storage.

*3.2.2. Experimental specimens (**IV–V, Thesis summary**)*

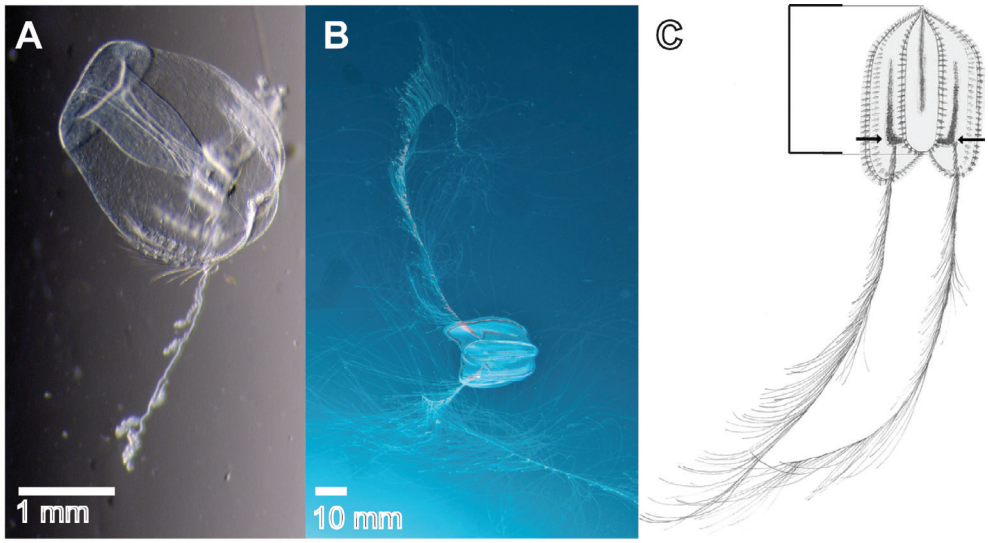
Mertensia ovum individuals used in the experiments were collected from the Arctic (with 3 l plastic buckets) (**IV**, **Thesis summary**) and from the Baltic Sea (WP-2 closing net: Hydrobios, Kiel, mesh size 180 µm, opening 0.25 m^2 with a non-filtering cod end) (**V**, **Thesis summary**) 1–2 days prior to the start of the experiments, allowing time for sorting and acclimation of the animals. Individuals were maintained in an incubator under *in situ* conditions and fed with the natural plankton collected from the same site to maintain the good condition of the animals. Also, a temperature-controlled laboratory area was used for handling and microscopy, as well as cooling bags for material transport to avoid temperature shock of the experimental animals during preparation.

Calanus spp. used as prey in the feeding and tolerance experiments with the Arctic population were collected by vertical hauls with WP-3 nets (Hydrobios, mesh size 1 mm, opening 1 m^2 fitted with a filtering 30 l cod end) from the bottom to the surface and maintained under *in situ* conditions to ensure their healthy condition (**IV**, **Thesis summary**). Even though a subsample of the sorted experimental prey stock was identified based on the stage-specific length relationships established by Kwasniewski et al. (2003) these three *Calanus* species (*C. glacialis*, *C. finmarchicus* and *C. hyperboreus*) were treated as *Calanus* spp. due to the difficulty and uncertainty associated with sized-based identification (Parent et al. 2011).

Mesozooplankton prey used in the Baltic Sea feeding experiments (copepodites of *Eurytemora affinis* and a natural assemblage of calanoid copepod nauplii) were picked from zooplankton samples collected with a WP-2 closing net (Hydrobios, Kiel, mesh size 180 µm, opening 0.25 m^2 with a non-filtering cod end) from the study sites (**V**). As microzooplankton prey, *Mesodinium rubrum* originating from a culture kept at Woods Hole Oceanographic Institution (USA), was used. The picoplankton prey was the picocyanobacterium *Synechococcus bacillaris* from a culture kept at Stockholm University (Sweden). A natural plankton assemblage was used as prey in the tolerance experiments with the Baltic Sea population, and was collected from the study site with a WP-2 net (Hydrobios, Kiel, mesh size 90 µm, opening 0.25 m^2 with a filtering cod end) (**Thesis summary**).

*3.2.3. Hydrological data (**I–V, Thesis summary**)*

Temperature, salinity, oxygen, and fluorescence data were collected from the whole water column at all sampling stations in both Arctic and Baltic Sea locations (**I–V**, **Thesis summary**).



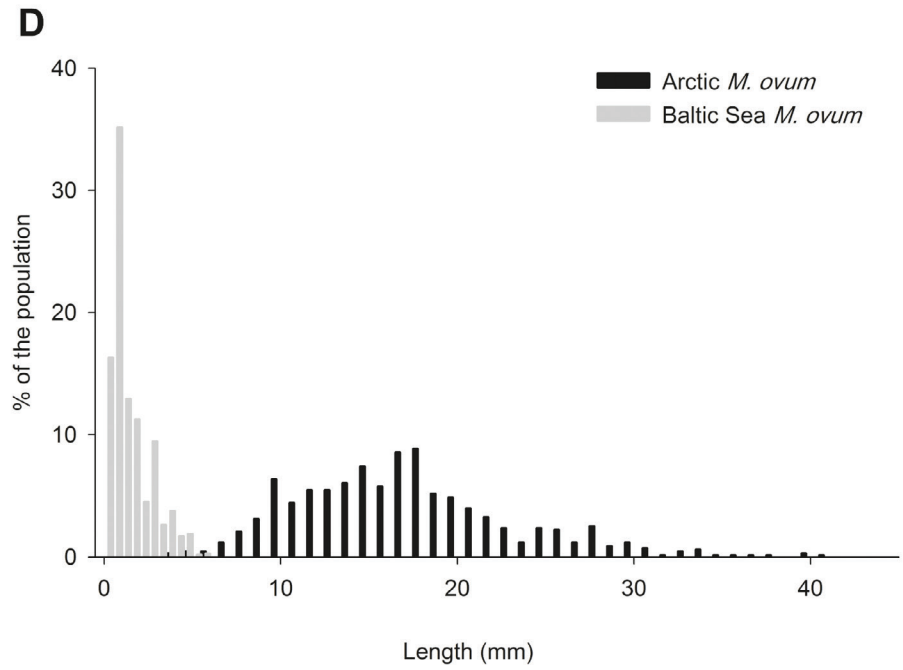


Fig. 3. Average size difference between *Mertensia ovum* in the Baltic Sea and in the Arctic. A) *M. ovum* in the Baltic Sea, scale bar 1 mm (photo M. Lehtiniemi); B) *M. ovum* in the Arctic, scale bar 10 mm (photo P. Leopold); C) Oral–aboral length measured from oral- to anal opening (not including the keels) indicated by vertical bar (modified from Lundberg et al. 2006 Fig. 2; D) Size distribution of the Baltic Sea population (gray), mean length 1.4 ± 1.1 mm, and Arctic population (black), mean length 17.2 ± 0.6 mm.

3.3. Morphological species identification (I–V, Thesis summary)

Ctenophore specimens were immediately sorted, photographed alive either onboard in glass aquaria or *in situ* while scuba diving (all specimens in the Arctic and a random set in the Baltic used for molecular species identification), and examined under a microscope (**I–V**, **Thesis summary**). For morphological species identification, special characters were observed based on, for example, Mayer (1912), Mortensen (1912), Greve (1975), Harbison (1985), Harbison & Madin (1982), Mills (1987a, b), Wrobel and Mills (1998), Mills and Haddock (2007), and Gershwin et al. (2010).

3.4. Molecular species identification

*3.4.1. DNA Extraction (**I-III**, **V**)*

To identify the species present, all specimens which had different characteristics from *M. ovum*, and a random set of at least 30 individuals per location, were preserved in four different ways: (1) frozen at -20 ºC, (2) dried for 24 h at 60 ºC and then frozen at -20 ºC, (3) air-dried on filter paper at ambient temperature, and (4) formalin-preserved for molecular identification (**I–V**). In addition, 8 archival ctenophore samples collected in the Bothnian Sea in 1990 and identified as *Pleurobrachia pileus* based on their appearance, mainly based on their body shape (P. Välipakka, unpubl. data) were used for molecular species identification (**II**). These samples had been counted, measured, individually dried on GF/F filters for 24 h at 60 °C, and stored at -20 °C for 19 years.

From all the samples, DNA was extracted from tissue with a modified Chelex rapid-boiling procedure (Walsh et al. 1991, Giraffa et al. 2000, Jarman et al. 2000) (**I–III**, **V**). The DNA was stored at 4 °C for up to 2 months. Concentrations of total DNA and purity were determined before the PCR amplifications with a Nanophotometer™ (Implen).

*3.4.2. Polymerase chain reaction and sequencing (**I–III**, **V**)*

The polymerase chain reaction (PCR) was used to amplify 18S rRNA genes and the ITS region. The amplification was performed with published primers or with primers designed for this study (Table 1) using polymerases provided by several manufacturers. The denaturation and annealing temperature and time, extension time, and number of cycles varied depending on the length of the amplified region and the polymerase. PCR products were purified using the Montage PCR96 Cleanup Kit (Millipore) according to the manufacturer's instructions (**I–III**). In the molecular analysis of the stomach contents, a real-time qPCR assay was applied using general *Synechococcus* sp. primers and a hydrolysis probe to quantify *Synechococcus* spp. in ctenophore samples, reference samples, and seston (Table 1, **V**, Becker et al. 2000). Reactions were performed in triplicate using the TaqMan Gene Expression Master Mix (Applied Biosystems) and a StepOne real-time cycler (Applied Biosystems). For more information, see the methods section of study **V**.

*3.4.3. Sequencing and sequence quality (**I–III**)*

Cycle sequencing of the PCR products was carried out using the cycling conditions of the

Big Dye™ terminator (Applied Biosystems, Foster City, CA, USA). The samples were loaded on a 3730xl automated sequencer (Applied Biosystems) at Macrogen Inc, Seoul, Korea (**I**, **III**), or an ABI 3730 PRISM® DNA Analyzer at KIGene (Karolinska Institute, Stockholm) (**II**).

The resulting nucleotide sequences were assembled using BioEdit software (Hall 1999), and electropherograms were checked by eye for poor base calls and sequence quality using Chromas Lite 2.1 (Technelysium Pty Ltd). The sequences have been deposited in the European Molecular Biology Laboratory (EMBL) Nucleotide Sequence Database.

*3.4.4. Alignment of sequences (**I–III**)*

DNA amplification, cloning, and sequencing were conducted in order to carry out phylogenetic analyses based on the DNA sequences. The good quality sequences were aligned using the program MAFFT (Katoh et al. 2002, Katoh & Toh 2008) with the Q-INS-i strategy, which takes the RNA secondary structure into account, and with a default gap-opening penalty of 1.53 and a default gap-extension penalty of 0.123. All *Mertensia ovum* specimens were aligned against Baltic *M. ovum* (GenBank accession number FJ668937, Gorokhova et al. 2009) and/or Arctic *M. ovum* (GenBank accession number AF293679, Podar et al. 2001) (**I–III**) to confirm the product identity. In the species identification, specimens were aligned against all possible ctenophores found in NCBI GenBank. All alignments were visually checked and adjusted.

*3.4.5. Generation of phylogenetic trees (**I, III**)*

Maximum likelihood bootstrap support values were calculated for the 18S rRNA gene and ITS1 region, and concatenated data (18S+ITS1) using GARLI (Zwickl 2006) with selected models from jModelTest (Posada 2008). Posterior probabilities were calculated using MrBayes 3.2 (Ronquist et al. 2012).

The trees were rooted using *Aurelia aurita*, *Aegina rosea*, *Tripedalia cystophora*, and *Microhydrula limopsicola* as out-groups (**I**, **III**). By definition, an out-group is a group of organisms that is closely related to the group of interest, but less closely than those inside the group of interest. This assumes that the out-group diverged first from the ancestral group before the group of interest during the course of evolution.

3.5. Experimental methods

*3.5.1. Feeding experiments (**IV–V**)*

Functional response feeding experiments were conducted with *M. ovum* specimens from the Arctic Ocean (**IV**) and the Baltic Sea (**V**). The experiments were conducted in temperature-controlled conditions using ambient temperature and salinity. Experimental water was collected from the same location as *M. ovum* specimens and filtered through a 50-µm (**IV**) or a 0.22-µm filter (**V**), depending on the sea of origin. Experimental vessels were selected using the ratio of container volume to ctenophore volume (1:2500) recommended by Purcell (2009) to limit the errors caused by the container effect.

Table 1. The oligonucleotide primers used for PCR in the thesis.

Primer	Target species	Sequence (5' to 3')	Main target region	Reference	Used in paper
18SF	universal	CTGGTTGATCCTGCCAGTAGT	18S rRNA	Kober and Nichols 2007	I, II, III
18SR	universal	GCAGGTTCACCTACAGAAACC		Kober and Nichols 2007	I, II, III
18SM	universal	GTGTACTGATCGATCTGTTC	18S	Paper III	I, III
M1F	*M. ovum*	CGCCGAAAACTTGCTCAAAC	ITS1	Gorokhova et al. 2009	I, II, III
M1R	*M. ovum*	CCGAGCGACAGATCGGATAC		Gorokhova et al. 2009	I, II, III
M2F	*M. ovum*	GTGCTGATTACGTCCCTGCC	ITS1	Gorokhova et al. 2009	I, II, III
M2R	*M. ovum*	CCCACGGACGATTTAACGAA		Gorokhova et al. 2009	I, II, III
PPIF	*P. pileus*	CGTAGGTGAACCTGCGGAAG	ITS1+5.8S rRNA	Gorokhova et al. 2009	I, II, III
PPIR	*P. pileus*	GCTCGGGGATCGCTCTACTT		Gorokhova et al. 2009	I, II, III
PP2F	*P. pileus*	AGACTTCATCGTGCTGGGGA	18S rRNA+ITS1	Gorokhova et al. 2009	I, II, III
PP2R	*P. pileus*	GTTAGGCCAACCCCGAAGAC		Gorokhova et al. 2009	I, II, III
ML1F	*M. leidy*i	TCGATGAAGAACGCAGCAAA	ITS1+5.8S rRNA	Gorokhova et al. 2009	I, II, III
ML1R	*M. leidyi*	GAACCCTTTCCAGTCGTCCC		Gorokhova et al. 2009	I, II, III
ML2F	*M. leidy*i	TAGGTGAACCTGCGGAAGGA	ITS1+5.8S rRNA	Gorokhova et al. 2009	I, II, III
ML2R	*M. leidy*i	CTTCGGACATCCTGCAAAGC		Gorokhova et al. 2009	I, II, III
1400F	universal	TGYACACACCGCCCGTC	ITS1	Podar et al. 2001	I, II, III
5'28Sr	universal	CTTAAGTTCAGCGGGTAGTCTCG		Podar et al. 2001	I, II, III
P100PA	*Synechococcus* sp.	GGTTTAGCTCAGTTGGTAGAGCGC	ITS1	Becker et al. 2000	V
P3	*Synechococcus* sp.	TTGGATGGAGGTTAGCGGACT		Becker et al. 2000	V
		5′ FAM to TAMRA 3'			
S100A	hydrolysis 1 probe	CTTTGCAAGCAGGATGTCAGCGGT		Becker et al. 2000	V

Prior to the experiments, individuals were sorted into a predetermined oral–aboral axis size class (approx. 1.8–2.2 cm in the Arctic and approx. 2–3 mm in the Baltic). Mesozooplankton prey were individually picked using a wide-bore pipette under a dissecting microscope, whereas *Synechococcus bacillaris* and *Mesodinium rubrum* were added from cultures with known densities to achieve the experimental concentrations.

The incubation time, bottle volume, and prey density were optimized in order to resolve a statistically significant feeding signal without suffering from prey depletion (**IV–V**, Gifford 1993, Båmstedt et al. 2000). The behavior of individual predators and prey was observed, and for *Calanus* spp. prey the time when the first *Calanus* spp. was eaten was recorded as the search time. Incubations were stopped by checking the condition of the predator and by either removing the predator (**IV**) or adding the fixative, which allowed the predator to dissolve into the experimental vessel (**V**) to limit the removal of extra prey from the experiments. The remaining prey were fixed in 25 % glutaraldehyde (final concentration 4 %) or in 4 % formalin-seawater buffered with hexamine (*Calanus* spp. and *S. bacillaris*), or in acid Lugol (*M. rubrum* and mesozooplankton). To be able to interpret predation efficiency, the remaining prey organisms were counted and identified and both the ingestion rate (prey predator^{-1} h^{-1}) and clearance rate (l predator^{-1} h^{-1}) were calculated. For more detailed information, see Table 2 and the methods section of studies **IV** and **V**.

In the Arctic, the predation impact (%) was calculated using the ingestion rates, *in situ* predator abundance, and *in situ* prey density from zooplankton samples from the field (**IV**). While calculating the predation impact, full overlap of predators and prey and constant predation were assumed. The potential predation impact of *M. ovum* aggregations on high-density prey accumulations was calculated using modeled predator and prey densities (**IV**).

In the Baltic, the degree of spatial distribution overlap (%) was determined for *M. ovum* and its potential prey items based on Lloyd's mean crowding on species 1 by species 2 (Lloyd 1967). The overlap was calculated separately for each prey group and depth layer using the high-resolution vertical samples (**V**).

*3.5.2. Tolerance experiments (**Thesis summary**)*

Salinity and temperature tolerance treatments were chosen to cover a wide range of recorded physical conditions in sampling conducted during 2008–2011 in the Baltic Sea and Arctic. In addition, salinities (< 5 in the Baltic Sea and < 30 in the Arctic) and temperatures (> 8 ºC in the Arctic) were chosen to represent predicted climate change scenarios. Predicted climate change scenarios used were based on two greenhouse gas emission scenarios (B1 and A2, IPCC 2007). A2 is a pessimistic scenario, assuming an increase in CO_2 with a similar rate to that currently observed, and 2.0–5.4 ºC projected global average surface warming, whereas scenario B1 predicts warming by only 1.1–2.9 ºC. In the Baltic Sea, the *M. ovum* population was clearly limited by the temperature of 10 ºC (**II**), which was the same as the critical upper limit for the temperature tolerance in the experiments with the Arctic *M. ovum* population. Thus, temperature experiments were not conducted with the Baltic Sea specimens. Additional

Table 2. Experimental design of feeding experiments conducted with *Mertensia ovum* as a predator both in the Baltic Sea and in the Arctic Ocean. Carbon values: *Eurytemore affinis* (Postel et al. 2007), Copepod nauplii (Granhag et al. 2011), *Mesodinium rubrum* (Johnson et al. 2007) and *Synechococcus bacillaris* (Mullin et al. 1966).

Location	Prey type	Prey carbon weight g C ind^{-1}	Container volume l	No. predator container^{-1}	Prey density ind l^{-1}	Prey density g C l^{-1}	Prey recovery %	No. experiment replicates	Temp C	Salinity	Duration h
Baltic Sea	*E. affinis*	0.951	1000	1	0.02	8.5	99.0	3	4	6	12
‘’	Nauplii	0.172	200	1	0.05	19.0	97.5	3	‘’	‘’	‘’
‘’	*M. rubrum*	0.000563	200	3	6.0	0.003		5	‘’	‘’	5
‘’	‘’	‘’	‘’	‘’	9.0	0.006		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	23.0	0.013		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	55.0	0.03		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	63.0	0.04		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	83.0	0.05		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	133.0	0.08		‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	‘’	180.0	0.1		‘’	‘’	‘’	‘’
‘’	*S. bacillaris*	0.0000254	200	3	21892.0	0.005		5	‘’	‘’	‘’
‘’	‘’	”	‘’	‘’	38429.0	0.01		‘’	‘’	‘’	‘’
‘’	‘’	”	‘’	‘’	41123.0	0.01		‘’	‘’	‘’	‘’
‘’	‘’	”	‘’	‘’	75399.0	0.02		‘’	‘’	‘’	‘’
‘’	‘’	”	‘’	‘’	335630.0	0.08		‘’	‘’	‘’	‘’
‘’	‘’	”	‘’	‘’	727947.0	0.18		‘’	‘’	‘’	‘’

Location	Prey type	Container volume l	No. predator container^{-1}	Prey density ind l^{-1}	Prey recovery %	No. experiment replicates	Temp C	Salinity	Duration h
Svalbard	*Calanus spp.*	5	1	0.2	100	5	4	32	5
‘’	‘’	‘’	‘’	1.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	2.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	4.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	5.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	10.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	20.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	30.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	50.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	‘’	100.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	20	1	2.0	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	2	‘’	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	5	‘’	‘’	‘’	‘’	‘’	‘’
‘’	‘’	‘’	10	‘’	‘’	‘’	‘’	‘’	‘’

experiments were conducted by decreasing and increasing the salinity by one unit every 24 h for both populations.

Experimental specimens were sorted into predetermined oral–aboral axis size classes (same as in feeding experiments) using a wide-bore pipette under a dissecting microscope. These individuals were isolated in 16.8 ml 6-well plates (Millipore) for the Baltic Sea population and 5 l plastic containers for the Arctic population containing the test solution. For the experimental set up, *in situ* sea water (< 20 µm) and Instant Ocean® solution (*in situ* temperature) were mixed to obtain the experimental salinities. For temperature experiments, thermo-controlled rooms were used. 6–24 replicates were included in each temperature and salinity experiment. The condition and behavior of the specimens were examined every 1–2 h during the first 24 hours, and then every 12 hours to record the length and number of deaths. Animals were fed daily with the natural plankton (<90 µm) assemblage in the Baltic Sea and *Calanus* spp. in the Arctic to reduce the degree of mortality due to food limitation. Fresh treatment solutions were prepared every 72 h, with the specimens being transferred to clean jars using either a wide-mouth pipette or a 30 ml jar.

3.6. Modeling the impact of future climate change (Thesis summary)

To assess the potential impact of changes in sea temperature and salinity in the Baltic Sea on the *M. ovum* population by the end of the 21st century, the climate scenario simulations were conducted by Dr Markus Meier at the Swedish Meteorological and Hydrological Institute. The climate scenarios used were the same as for the tolerance experiments, and as for future predictions for the Arctic. Following Meier et al. (2011) Meier, Andersson et al. (2012), Meier, Müller-Karulis et al. (2012), regionalized data were used with the forcing calculated by applying a dynamical downscaling approach using the regional climate model RCAO (Rossby Centre Atmosphere Ocean model, Döscher et al. 2002), with lateral boundary data from HadCM3 (Hadley Centre in the UK, Gordon et al. 2000) and ECHAM5 (Max Planck Institute for Meteorology in Germany, Roeckner et al. 2006, Jungclaus et al. 2006). In the study, the three-dimensional circulation model RCO (the Rossby Centre Ocean model) was used with a horizontal resolution of 3.7 km and with 83 vertical levels (3-m layer thicknesses). However, the focus was on the main occurrence area of the *M. ovum* population, i.e. the water mass where salinity is ≥ 5.5 and temperature <7 ºC during all seasons in all areas of the Baltic Sea (**II**, **Thesis summary**).

In the Arctic, the *M. ovum* population has been described to tolerate a wide range of salinity changes (28-40; **Thesis summary**) and occurrence is temperature limited (constantly below 10ºC; Percy 1989, Eiane & Tande 2009). Thus, to assess the potential impact of future changes only sea surface temperature (SST) was taken into consideration contemplating decadal changes in sea surface temperature and in the isotherm 9–10 ºC. Both observed (1960–2005) and projected (1990–2100) sea surface temperature images were used according to IPCC 2001 and Beaugrand et al. (2008). The focus was on the known occurrence area of the *M. ovum* population in the European side of the Arctic.

3.7. Statistical analysis (I–V, Thesis summary)

All statistical analyses (presented in more detail in each study) were performed using the statistical program R, version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria), applying a significance level of 0.05.

4. RESULTS AND DISCUSSION

4.1. Ctenophore species identification

The first part of this thesis research included three taxonomic studies of ctenophores living either in the Arctic Ocean or in the vicinity of the Baltic Sea. Here, the results of these three studies (**I–III**) are presented and discussed with the current taxonomic knowledge of ctenophores.

4.1.1. Problematic morphological species identification

During the sampling conducted in the Arctic, it was clearly noted that adult cydippid ctenophores, both captured in the samples and observed while scuba diving, exhibited morphologies that differed from the species previously known to occur in this area (**1**). Large numbers of synapomorphies were present, and the main identifiable morphological differences were in the body shape, structure of the tentacles, and length of the comb rows (Fig. 4, Table 3). For the specimens identified similar to a yet undescribed mertensiid (Plate 73 D in Mills & Haddock 2007), the body shape was oval in the tentacular plane and considerably compressed in the sagittal plane (Fig. 4C, A9 in Fig. 6, accession number HF912439). They also had shorter tentacles and secondary tentilla, and the whole-body-length comb rows contained longer cilia, giving a "furry" appearance. The specimens identified as *Euplokamis* sp. (as described in Mills 1987a) had a more elongated circular body (larger length-to-width ratio) (Fig. 4A, G1 in Fig. 7, HF912430) with ctene rows constituting approximately ¾ of the total length and the few secondary tentilla on the tentacles were held tightly coiled, giving the tentacle a beaded appearance. Morphologically, *M. ovum* (Fig. 4D and E, Fig. 7 [A8, F2 and B10], HF912437, HF912435, HF912434, HF912433) and *P. pileus* (Fig. 4F) of the same size class differ by having a different body shape (strongly compressed in the sagittal plane for *M. ovum* and more egg-shaped or almost spherical for *P. pileus*), more numerous secondary tentilla, all of which are uncoiled, and comb rows starting near to the aboral pole and extending more than ¾ of the distance towards the mouth (e.g. Mayer 1912, Mortensen 1912). Also, *Dryodora glandiformis* differs by having an acorn-shaped, nearly cylindrical in cross-section body shape with tiny unbranched tentacles, comb rows extending ½ the body length and a large "vestibular area" where prey is held prior to ingestion (e.g. Wrobel & Mills1998).

Morphologically different specimens were also observed during the sampling for *M. leidyi* and *M. ovum* near the entrance to the Baltic Sea (**III**). The specimens identified as *Euplokamis* sp. (as described in Mills 1987a) had an unpigmented and elongated (larger length-to-width ratio) body, tentacles had fewer side branches than *M. ovum*, which were coiled except when capturing prey, and the ctene rows constituted approximately ¾ of the total length (Fig. 4H, HE647719, HE805698, HE805699). The larval

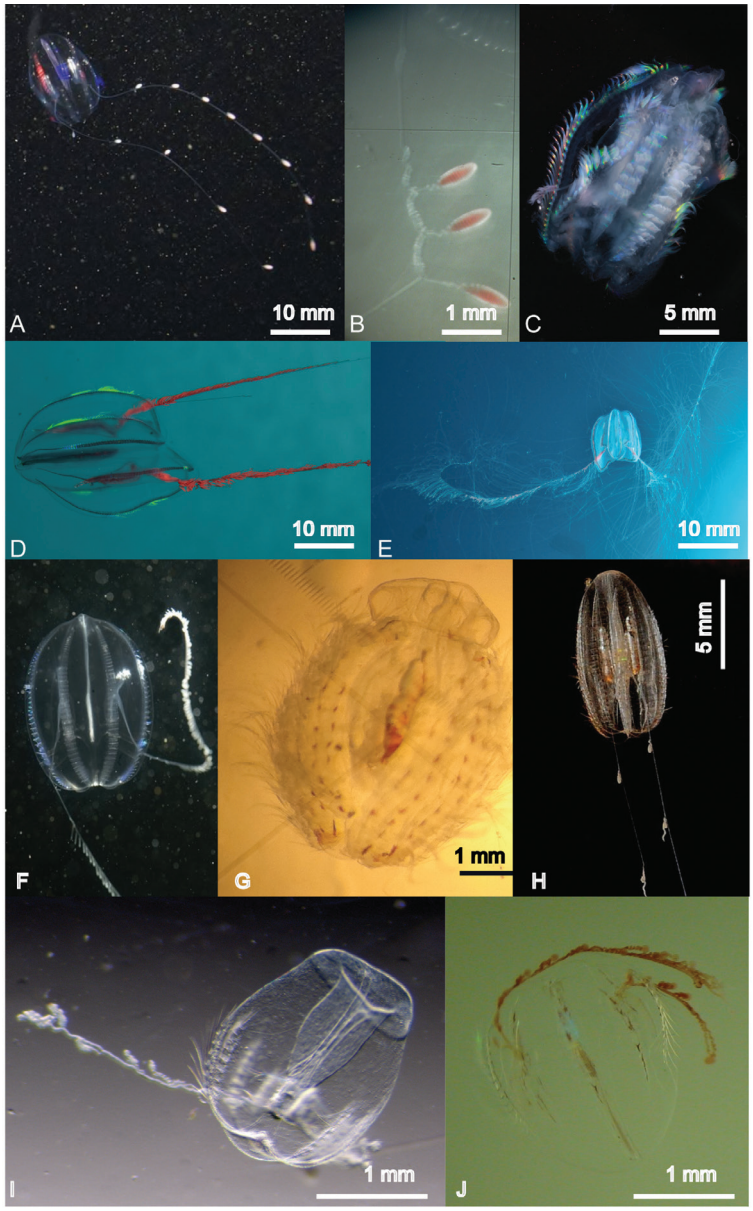


Fig. 4. A) *Euplokamis* sp. from the Arctic, HF912430 (photo G. Johnsen); B) Coiled tentacle of *Euplokamis* sp. from the Arctic, HF912430 (photo S. Majaneva); C) Unidentified mertensiid from the Arctic, HF912439 (photo S. Cochrane); D) *Mertensia ovum* from the Arctic, HF912437 (photo P. Leopold); E) *Mertensia ovum* with stretched tentacles/tentillas from the Arctic, not sequenced (photo P. Leopold); F) *Pleurobrachia pileus* from unidentified area (photo M. Decleer, WoRMS); G) *Euplokamis* sp. (larvae) from adjacent waters of the Baltic Sea, cultivated as adult (photo L. Granhag); H) *Euplokamis* sp. (adult) from adjacent waters of the Baltic Sea, HE647719 (photo S. Gotensparre); I) *Mertensia ovum* from the Baltic Sea, FJ668937 (photo M. Lehtiniemi); J) Unidentified mertensiid from the Arctic, not sequenced (photo S. Majaneva).

Table 3. Morphological characteristics together with Photo ID and sequence reference number of the cydippid ctenophores, *Mertensia ovum*, unidentified mertensiid and *Euplokamis* sp., found in this thesis from the coastal Svalbard and from the Baltic Sea.

Location	Taxa	Size	Body shape	Color	Location of tentacle exit	Length of tentillas	No. of tentillas	Length of comb rows	Cilia	Photo ID	Sequence
Arctic	undescribed mertensiid	app. 20 mm	Oval in the tentacular plane, compressed in the sagittal plane	Transparent, red/pink color along the comb rows	1/4 body length from the aboral pole	Short, ½ of body length	-	Total body length	Long (furry appearance)	Fig. 4C	HF912439
	Mertensia ovum	> 75 mm	Oval in the tentacular plane, strongly compressed in the sagittal plane	Transparent, red/pink color along the comb rows	1/4 body length from the aboral pole	Long, 10-20 times body length	Numerous	> 3/4 of body length	Raised up on ridges, equal length	Fig. 4D and E	HF912437 HF912435 HF912434 HF912433
	Euplokamis sp.	20-30 mm	Elongated circular body (larger length to width ratio)	Transparent, red pigment at edges	Close to aboral pole	Long, 10-20 times body length	Few, often tightly coiled (a beaded appearance)	2/3-3/4 body length	Equal length	Fig. 4A	HF912430
Baltic Sea	*Mertensia ovum*	< 10 mm	Egg shape	Transparent	1/4 body length from the aboral pole	1-2 times body length	few	1/2 body length	Equal length	Fig. 4I	FJ668937
	Euplokamis sp.	3-12 mm	Elongated circular body (larger length to width ratio)	Transparent body, unpigmented or lightly pink tentacles	Close to aboral pole	Long	Few, often tightly coiled (a beaded appearance)	3/4 body length	Equal length, larvae have long (furry appearance)	Fig. 4G and H	HE647719 HE805698 HE805699

specimens collected typically had red dots along comb rows and large tightly-packed cilia, giving a "furry" appearance (Fig. 4G, see detailed photos in Fig. 2 of article **III**) that differed from other ctenophore larvae, such as *M. leidyi*/*Bolinopsis infundibulum* and *Beroe* spp., or from the larvae or small-sized adult ctenophores of *P. pileus*/*M. ovum* (Fig. 4I [FJ668937]).

Quite often, individuals were severely damaged during sampling, allowing only some of their unique characters to be seen and hindering more detailed examination under the microscope (Fig. 5). Thus, characteristics such as the shape of the mouth and tentacle bulbs, meridional canals, and the structure of the gut or gonads (e.g. Harbison & Madin 1982 and references therein, Harbison 1985, Wrobel & Mills 2003, Lindsay & Miyake 2007, Mills & Haddock 2007) were often excluded as identification features. Obtaining large intact specimens was difficult (see also: e.g. Alldredge 1984, Pugh 1989, Harbison 1992, Dennis 2003, Haddock 2004); tentacles often came loose during sampling, limiting identification based on tentacles or tentacle bulb characteristics (Fig. 5E, F and G). With the most fragile specimens, the body was often torn into pieces (Fig. 5G). Besides the damage caused by nets, specimens were often impaired if not treated immediately after sampling. In some cases, even a standing time of only 10–15 minutes allowed specimens to shrink and become unrecognizable (Fig. 5E) and these unrecognizable, fragmentary remains of ctenophores were cemented together with several copepods and other taxa in the samples. Also, the use of conventional preservatives caused a similar effect (Fig. 5A, B and D, Harbison et al. 1978). From these images, it is evident how little light this piece-by-piece research was able to shed on the identification, especially at the species level.

During the sampling for this thesis, specimens collected and photographed by scuba divers (or by hand using buckets) were in the best condition for species identification, even though in photographs the small detailed morphological characters usable for identification were limited (Fig. 4). This is consistent with the recommendation to use Remote Operated Vehicle (ROV) and other submersibles for the *in situ* identification of gelatinous zooplankton such as ctenophores (e.g. Graham et al. 2001, Båmstedt et al. 2003, Haddock 2004, Lindsay & Miyake 2007, Purcell et al. 2010, Raskoff et al. 2010). Raskoff et al. (2010) provided a baseline for understanding the biodiversity and distribution of gelatinous zooplankton in the Arctic Ocean, with detailed ROV observations combined with multiple plankton sampler tows. Whereas identification to the species level was possible for many taxa (mainly cnidarians) due to the high quality of the video, relatively low number of macroscopic species occurring in the area and synapomorphies among the species, it was challenging with the ctenophores (Raskoff et al. 2010). In addition, some taxa were observed several times in ROV images, but none of these specimens were collected with the net for closer examination or for molecular species identification (see also Mills 1987a, Lindsay & Miyake 2007). Thus, video analysis and other optical *in situ* methods do not solely resolve the challenges of the morphological identification of ctenophores to species level.

Species identification of ctenophores is challenging not only due to damaged and unpreservable specimens, but also because the scientific literature on ctenophore taxonomy and classification is widely

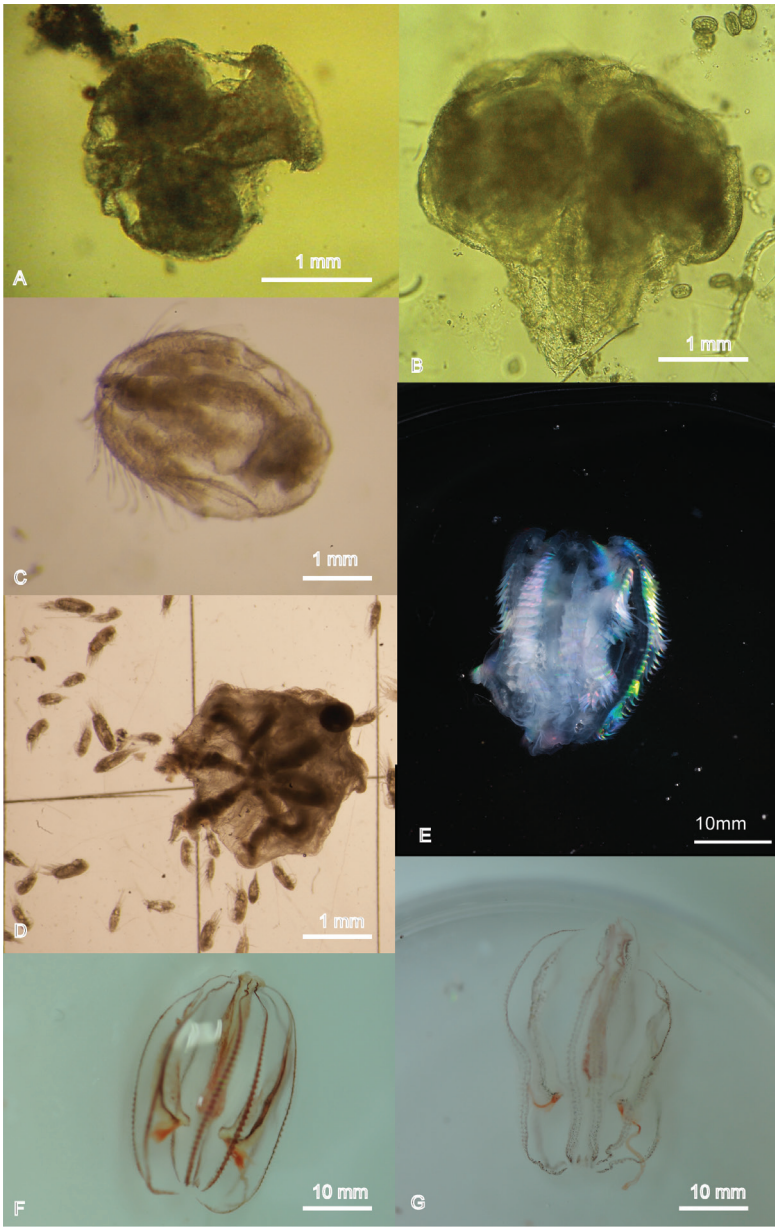


Fig. 5. A) Ctenophore sp. in formalin, not sequenced (photo E. Gorokhova); B) Ctenophore sp. in formalin, not sequenced (photo E. Gorokhova); C) Ctenophore sp. in formalin, not sequenced (photo A. Båtnes); D) Ctenophore sp. in formalin, not sequenced (photo A. Båtnes); E) Unidentified mertensiid from the Arctic, live specimen, HF912439 (photo S. Cochrane); F) Unidentified cydippid ctenophore, live specimen, not sequenced (photo S. Majaneva); G) *Mertensia ovum* from the Arctic, HF912437 (photo S. Majaneva).

dispersed, and much of it is difficult to locate. The information may also be outdated and overlapping. Mills (Mills 2013) has done an excellent job of listing nearly 200 ctenophore species names that appear to be valid today, including now-synonymized names ("nominal") that are no longer in active use, e.g. *Mnemiopsis leidyi*, *M. gardeni* and *M. mccradyi* (Seravin 1994, Reusch et al. 2010 and references therein). For *M. ovum, Mertensia cucullus* (Agassiz 1860) is a known synonym, but *Callianira compressa* (Mertens 1833) and *Euplokamis octoptera* (Mertens 1833) are also likely to be *M. ovum* (Mills 2013). However, these and possibly other nominal species descriptions are difficult to trace. While some of the species descriptions for *M. ovum* unmistakably describe some other species (see e.g. Plate 1, Fig. 1 in Mayer 1912, used also in Arctic Ocean Biodiversity project by Census of Marine Life [http://www.arcodiv.org]), descriptions for the species in the family Euplokamididae (note: Euplokamidae in NCBI and in Articles **I** and **III**) are limited. Thus, it is impossible to provide species-level identification for some of the specimens, such as *Euplokamis* sp. (**I**, **III**, see also e.g. Gershwin et al. 2010 for the order Cydippida).

For the species with existing descriptions, it is common for morphological characteristics to be well presented only for some of the life stages (typically adult stage) or size classes, as illustrated by the misidentification of the small sized *M. ovum* in the northern Baltic Sea (e.g. Gorokhova et al. 2009, Gorokhova & Lehtiniemi 2010). Cydippida are generally described as primitive forms of ctenophores (e.g. Podar et al. 2001) due to the "cydippid" larval stage of other orders. Thus, it might be that some larval stages of other orders have been described as cydippid species, or *vice versa* (Harbison & Madin 1982, Harbison 1985, Lehtiniemi et al. 2007). Baltic Sea ctenophore studies have clearly demonstrated that species identification is even more challenging for specimens in early life stages or for small-sized adults (<10 mm) than for larger adult ctenophores (e.g. Mayer 1912, Mortensen 1912, Podar et al. 2001, Gorokhova & Lehtiniemi 2010), while in the Arctic these small specimens, let alone eggs, are still completely excluded from the research conducted. In the southern Baltic Sea and in the adjacent waters, at least five ctenophore species were reported to occur prior to the first reports of *M. ovum* and *Euplokamis* sp. (*M. leidyi, P. pileus*, *B. infundibulum*, *B. cucumis* and *B. gracilis*; Greve 1975, Hansson 2006, article **III**). All of these, besides *Beroe* spp., are very similar in morphology at a small size or young age (tentaculate-stage larva; <5 mm). In addition, since the first reporting of *M. ovum* from the Baltic Sea, and before this thesis (see Table 3), the morphological characteristics of these small-sized specimens have not been reported. Thus, in article **II**, morphological species identification was not carried out, and identification solely relied on molecular methods.

Even though Oliveira & Migotto (2006) provide a benchmark for ctenophore identification studies, the lack of a description of the criteria for species and thus also life stage identification is a common problem in ctenophore studies, which makes results questionable (e.g. Kube et al. 2007, Lehtiniemi et al. 2007, Viitasalo et al. 2008, Javidpour et al. 2009a, b, Jaspers et al. 2012, 2013). For example, Jaspers et al. (2012) reported *M. ovum* to occur and reproduce only as a larval stage in the Baltic Sea. *Mnemiopsis mccradyi* is known to reproduce already in its cydippid stage, prior to its

gradual morphological transition to the final lobate stage (Martindale 1987). However, as *M. ovum* does not undergo a relatively abrupt change when growing, no proper definition is available for the larval stage of *M. ovum*. In addition, ctenophores, especially *M. ovum*, are known to be able to fast longer periods when food availability is limited, and hence, reduce their size significantly (e.g. Percy 1989). Thus, a small size alone is not a reliable indicator of the life stage, as a severe reduction in the size of a variety of marine species in low saline areas has been reported (Box 2).

To conclude, this thesis considered the severe challenges and limitations in morphological ctenophore identification. These well-known problems have occasionally arisen one after the other for decades without any changes in practice, and radical revision of species descriptions and methodologies is still in demand.

4.1.2. Do molecular identification methods solve the problems?

Most of the good-quality cydippid 18S rDNA sequences from the Arctic were identical (**I**), with a 99 % match with *M. ovum* (AF293679 and FJ668937) in a BLASTN search. Also, from the good-quality sequences of the ctenophore ITS1 region, most morphologically identified as *M ovum* had a 93–99 % match with *M. ovum* (FJ668937). The sequence of the cydippid specimen with shorter tentacles and secondary tentilla, and the comb rows with longer cilia, giving a "furry" appearance, had a 99 % match with the undescribed mertensiid sp. 3 (Fig. 1C in Podar et al 2001, AF293681). The sequences of specimens with an elongated body shape and coiled tentillae had a 99 % match with *Euplokamis* sp. found in the Baltic Sea (**I**, **III**, HE647719). Thus, the molecular methods confirmed the morphological identification of *Euplokamis* sp. near the entrance to the Baltic Sea and co-occurrence of two additional species, an undescribed mertensiid and *Euplokamis* sp., with *M. ovum* in Svalbard waters.

The 18S rDNA is known to be highly conserved among ctenophore species, with a maximum divergence between two species of 87 bp, i.e. less than 5 % (Podar et al. 2001, **I**, **III**). Podar et al. (2001) found close sequence similarity (only 2 bp differences at the level of 18S rDNA) between the Arctic *M. ovum* and an as yet undescribed mertensiid species (species 2, AF293680) inhabiting the tropics, even though these two species are morphologically distinct. Therefore, the 15-bp difference (99 % match) between individual A9 and the undescribed mertensiid sp. 3 (**I**) clearly implies that individual A9 was obtained from a species not sequenced earlier (Fig. 6). However, this conservatism makes the 18S rDNA gene an inappropriate marker at the species level.

The more variable ITS region has often been suggested for use in detailed species identification (e.g. Anderson & Adlard 1994). Recently, ITS1 was used for the identification of *M. ovum* within the Baltic Sea (Gorokhova et al. 2009). Thus, in article **II**, mainly *M. ovum*-specific primers for the ITS region were used (Table 1). In general, species identification was carried out by diagnosing the PCR products visualized on 1.5 % agarose gels stained with ethidium bromide, and only 10 randomly selected individuals were thus sequenced to confirm the visual identification. In the different areas of the Baltic Sea, 92–95 % of specimens were identified as *M. ovum*, while the remaining 5–8 % were either identified as *M. leidyi* or

did not produce any amplification, including reactions with universal primers. Most of the specimens not amenable for amplification originated from the formalin-preserved samples, and were thus specimens that failed in DNA extraction. In addition, ctenophore samples collected in 1990 revealed a 100 % match with *M. ovum* (FJ668937) in a BLASTN search. Therefore, it was concluded that all archival samples contained this single species and were most probably misidentified as *Pleurobrachia pileus* in earlier reports (e.g. Ackefors 1969, Vuorinen 1987).

The use of the ITS region in species identification could provide a simple standardized PCR-based assay. This method could be used to discriminate among morphologically similar ctenophore species, especially in areas with low ctenophore species richness such as the Baltic Sea. Nevertheless, the identification of ctenophore specimens to the species or genus level using the ITS region can be problematic due to the low number of published sequences, the lack of species-specific primers and protocols, and a general lack of worldwide material to examine (see also Wallberg et al. 2004). At the time of the first sequences of this thesis (2011), 17 ITS-region sequences were publicly available in GenBank, representing 9 different species within the whole phylum (4 belonging to the order of Cydippida). According to the similarity in the ITS1 sequences, the Baltic *M. ovum* population has been reported to be 97 % identical with that in the Arctic, but this is based on a single Arctic specimen (Gorokhova et al. 2009), and *M. ovum* was the only Mertensiidae for which the ITS1 had been sequenced before studies **I** and **III** (NCBI GeneBank 2011). Therefore, in most areas, this method would need further study to ensure the development of species-specific primers and to determine more accurately the levels of intraspecific and interspecific variation in the ITS1 region.

The lack of a comprehensive comparative molecular database (published sequences) and worldwide material against which unknown species can be compared became evident in the samples collected from the Swedish coast (**III**, NCBI GeneBank 2013, note also case *Beroe* sp. in Fig. 6 [C5] and Fig. 7 [H1]). The 18S rRNA BLASTN search revealed a 99 % match with *M. ovum* (e.g. AF293679), and the undescribed mertensiid sp. 2 (AF293680), and the sequences clustered together with these mertensiids in the consensus Bayesian tree (Fig. 6). For the ITS1 region, the BLASTN search revealed a lower sequence identity (91 %) with *M. ovum*. Nevertheless, the ITS1 sequences clustered together with *M. ovum* in the consensus Bayesian tree (100 % maximum likelihood bootstrap support, Fig. 7). Thus, the molecular results indicated that *M. ovum* was the closest relative, but the morphological characteristics pointed towards the family Euplokamididae (see above). *M. ovum* is the only species described and sequenced in the family Mertensiidae, and none of the species in the family Euplokamididae had been sequenced before. Since the variation within these families is unknown based on existing sequences, it cannot be determined from this analysis whether *Euplokamis* sp. belongs to a family of Mertensiidae or forms a separate family (family Euplokamididae), as has been morphologically described (Mills 1987a, b).

In article **I**, attempts were made to identify the Arctic and Baltic ctenophores using the barcoding gene (COI mtDNA), but with no success. Various PCR primers were used, including primers based on published sequences (e.g. Folmer et al. 1994, Ortman 2008) and specially designed from the only two existing ctenophore mtDNA sequences,

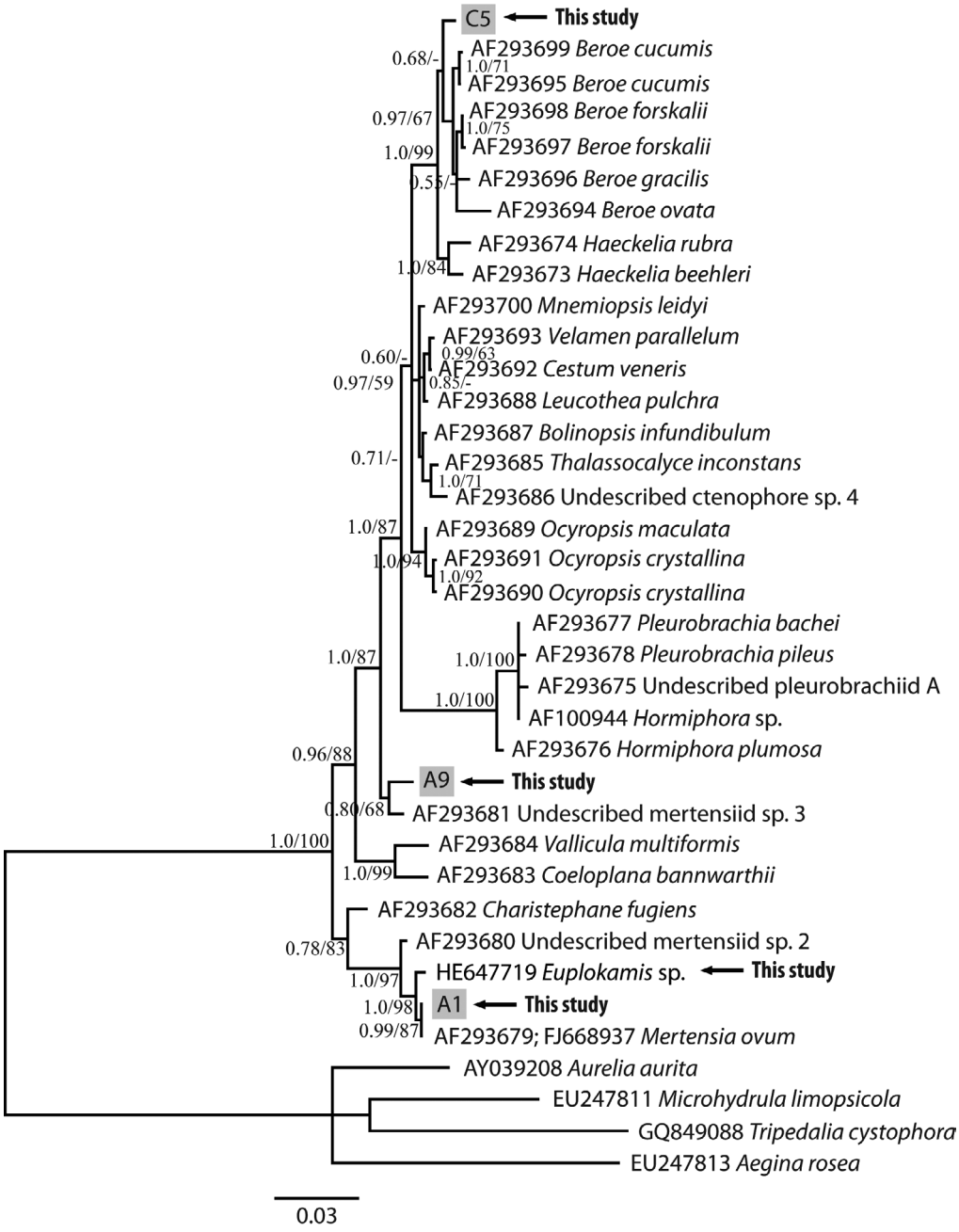


Fig. 6. Consensus Bayesian tree based on 18S rRNA gene sequences of members of ctenophores. The sequences are denoted with the sampled specimen numbers (sequenced within this study) or accession numbers (derived from GenBank). Posterior probabilities (left) and maximum likelihood bootstrap support values (right) are shown near the internal nodes. *Aurelia aurita*, *Aegina rosea*, *Tripedalia cystophora* and *Microhydrula limopsicola* as an out-group, and their support values are not shown.

P. bachei and *M. leidyi* (Pett et al. 2011, Kohn et al. 2012). Despite the tests with various species preservation methods, DNA extraction methods, sets of primers and PCR protocols, not a single specimen was amplified, even though the DNA used was of sufficiently good quality to be amplified with 18S or ITS1 primers. The lack of success suggests either a failure in the primer design, the special characteristics of the ctenophore mitochondrial genome, or more likely both (Pett et al. 2011, Kohn et al. 2012). While the barcode is certainly an effective tool for species identification for well-known, comprehensively sampled groups, for ctenophores it needs thorough taxonomical studies to generate the standards and protocols for establishing comparative databases, and to facilitate development of barcoding.

To conclude, a combination of morphological species identification and molecular methods revealed other cydippid ctenophore species and unidentified species co-occurring with the dominating *Mertensia ovum* in High Arctic waters (**I**). Similarly, the first sighting of the cydippid ctenophore, *Euplokamis* sp., in the mouth of the Baltic Sea was reported (**III**) in conjunction with *Mnemiopsis leidyi* and *M. ovum* during monitoring in the Baltic Sea. Interestingly, the absence of the cydippid ctenophore *Pleurobrachia pileus*, earlier reported to commonly co-occur with *M. ovum* in the High Arctic and to be present throughout the Baltic Sea (earlier reported as the only cydippid ctenophore species in the northern Baltic Sea), was not present in any of the samples in either study site collected between 2008–2011 (**I–III**).

The results of this thesis and articles **I–III** clearly emphasize the challenges in both morphological and molecular ctenophore species identification (not just Cydippida but other ctenophore orders too) and demonstrate that extensive revisions are still in demand, since the current molecular work conducted with ctenophores does not provide a clear solution. The challenges warrant the development of molecular assays that could be employed for ctenophore identification, and integrated in field studies. This thesis suggests that this will only be possible by combining both morphological and molecular approaches, as has recently been highlighted by McManus and Katz (2009). Further developments include sequencing more specimens in diverse locations together with proper morphological species descriptions and photographic IDs as described in Olivera and Migotto (2006).

4.2. Ctenophore detectability and abundance

The second part of this thesis included two studies aiming to describe the abundance of *M. ovum* in the Baltic Sea during different years, throughout the seasons and in different water masses (**II**), and the abundance of the Arctic population while estimating its patchy distribution (**IV**). Here, the main results of these two articles are presented.

In the extensive field surveys conducted during 2007–2012, *M. ovum* was found to occur throughout almost the entire Baltic Sea. The northern limit of distribution was the Quark, most likely due to the low salinity in this area (**II**, **Thesis summary**). The highest densities of *M. ovum* were found in the open sea area of the Bornholm Basin (68 ind m^{-3}, Fig. 2B). The species was not found in the westernmost areas near the Kattegat and Danish Straits. It remains unknown why *M. ovum* was not detected in the western parts of the Baltic Sea, where the salinity is higher and closer to the levels in the Arctic. Even

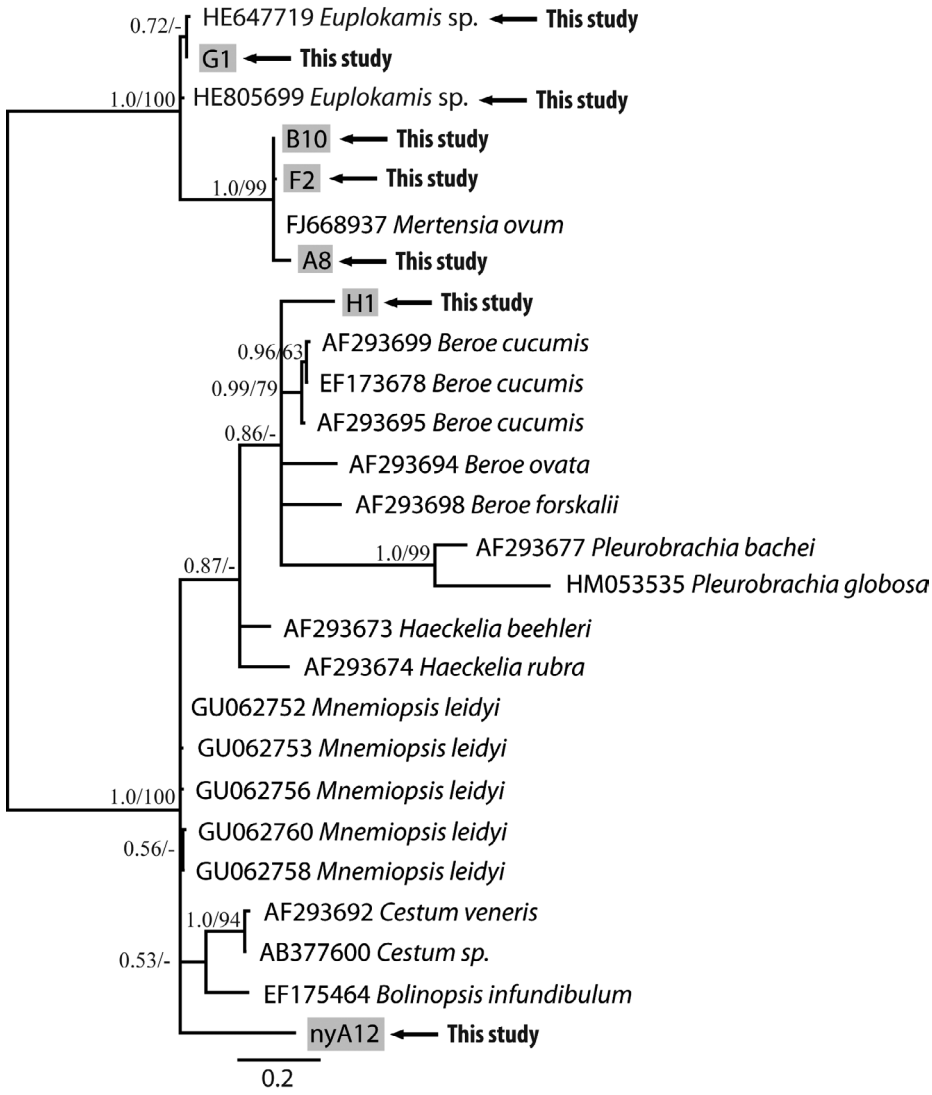


Fig. 7. Unrooted consensus Bayesian tree based on ITS region data of the members of ctenophores. The sequences are denoted with the sampled specimen numbers (sequenced within this study) or accession numbers (derived from GenBank). Posterior probabilities (left) and maximum likelihood bootstrap support values (right) are shown near the internal nodes.

though the temperature might be limiting factor for the distribution (see below) another explanation for the apparent absence may be insufficient sampling, which may have failed to capture species with a very low abundance. The more frequent monitoring of ctenophores at the entrance of the Baltic Sea after 2010 might be the reason for the first observations of *Euplokamis* sp. in the area (**III**). Due to insufficient sampling prior to this study, the invasive status of the species remains unclear.

In the Baltic Sea, the abundance of *M. ovum* varied naturally between areas, years and seasons, but also between replicated samples. Overall abundances of *M. ovum* were the highest from late autumn to early spring, decreasing to very low numbers in summer. The vertical distribution also varied seasonally, with maximum abundances commonly found in the coldest parts of the water column, in deeper water layers during the summer. In the winter, the distribution appeared to be more even compared with the summer, although the poor sampling resolution in the winter did not allow the testing of this trend at all study sites. The physical conditions of the water appeared to be significant components determining ctenophore abundance, with the highest abundances found in waters with oxygen concentrations > 4 ml l^{-1}, salinities ≥ 5.5 and temperatures below 7 °C (**II**).

Based on the field surveys conducted during 2008–2011 in the Arctic, *M. ovum* was present at all sampling locations around Svalbard (**I**, **IV**). The abundances (0.07 to 3.9 ind m^{-3}) were comparable to those reported in previous studies conducted in the same area (Swanberg & Båmstedt 1991a, b, Falk-Petersen et al. 2002, Lundberg et al. 2006). In Arctic waters, the highest abundances have been detected in the surface layers, mainly between 25 m and the surface during the summer-autumn, which is thought to be due to high availability of zooplankton prey (e.g. *in situ* observations, Raskoff et al. 2005, Lundberg et al. 2006; however see Percy 1989). Previously, *M. ovum* has been reported to descend to deeper waters for the winter, probably following prey (Siferd & Conover 1992). However, during the seasonal sampling in Billefjord in 2008–2009, *M. ovum* was observed in the surface waters throughout the winter, and in Kongsfjord during January 2010 both *M. ovum* and *Euplokamis* sp. were observed from the surface waters (unpubl. data). In the Arctic, it is important to note the limited seasonal resolution in sampling due to the harsh winter conditions.

The results of articles **II** and **IV** highlight that the seasonal and vertical distribution of this species in the Baltic Sea is very different from its main distribution in the Arctic. These differences are most probably related to the prevailing physical conditions. As *M. ovum* is a true marine, cold-water species (e.g. Blachowiak-Samolyk et al. 2008), it probably lives at the limit of its physiological tolerance in the brackish Baltic Sea (see also chapter 4.4). However, from these studies it was evident that the abundances of *M. ovum* were higher in the Baltic Sea compared with the maximum abundances reported from the Arctic: 3.9 ind m^{-3} in article **IV**, 12 ind m^{-3} in Resolute Passage (Siferd & Conover 1992), and 4.7 ind m^{-3} in Svalbard waters (Lundberg et al. 2006). Importantly, note that these abundances are probably underestimates, as ctenophore sampling is known to be challenging due to patchiness and the low efficiency of net sampling (**IV**), and that small specimens were completely excluded from research conducted in the Arctic.

A good example of the inaccuracy in ctenophore sampling is the high variation in *M. ovum* abundance between samples taken with the MultiNet and MIK net in the Arctic (**IV**), even though the samples were taken as simultaneously as possible. Also, the high variation in the numbers of individuals caught in each MIK-net tow at each sampling station points to a highly patchy distribution. A similar phenomenon was also observed during the sampling in the Baltic Sea (**II**). Therefore, these data

support the concept that this species is not evenly distributed through the whole water column, and that net sampling in general can lead to severe underestimations if the densities are calculated as an average. In addition, the small opening of the net, speed when towing, angle of the net and the mesh size may also contribute to the erroneous abundance estimates. For example, in the Arctic, zooplankton studies are often conducted with relatively coarse nets (500–1000 µm mesh size, e.g. Søreide et al. 2003, Lundberg et al. 2006, Purcell et al. 2010) causing larvae and small-sized individuals (<5 mm) to remain undetected (Fig. 3), and with nets with small opening ($0.5m^2 – 1m^2$, e.g. Søreide et al. 2003, Lundberg et al. 2006) allowing large specimens to escape.

Sampling is also usually conducted over depth scales that are too large to evaluate patchiness in different depth layers (Graham et al. 2001, Purcell 2009, Purcell et al. 2010, Raskoff et al. 2010). In the Arctic, small-scale patchiness of *M. ovum* was observed from both the Zodiac and during multiple dives at all sampling locations. *M. ovum* individuals were concentrated in the upper 10 to 20 m of the water column, where densities in patches were estimated to be >500 ind m^{-3} from visual counts (**IV**, S. Majaneva, B. Gulliksen & J. Berge pers. obs.). Unfortunately, these observations could not be substantiated by net sampling, as the observation area was not accessible by ship. Similar observations from ROVs and traditional net sampling have been reported from several locations around the Arctic, where up to 99 % of *M. ovum* have been found to occur in dense patches in the upper 25 m (Swanberg & Båmstedt 1991a, Purcell et al. 2010, Raskoff et al. 2010).

Further uncertainties in detectability caused by the common use of preservatives, such as formalin, creates a challenge when estimating ctenophore abundances and ecological roles because some fragile and/or small-sized specimens partly or completely dissolve when preserved for longer periods. The ctenophores collected within the HELCOM zooplankton monitoring were preserved in formalin and counted under a dissecting microscope within a year of collection (**II**). A significant decrease in specimen recovery in the preserved samples was detected, and abundance estimates from the preserved samples were recalculated with a correction factor.

Due to the scarcity of early reports and lack of long-term monitoring, it remains unclear whether the abundance and distributional patterns of *M. ovum* have changed in recent decades. In article **II**, *M. ovum* abundance data from the late 1980s and late 2000s were compared using published papers on summer abundances in the Gulf of Bothnia (Vuorinen 1987, Vuorinen & Vihersaari 1989). However, the difference in these comparisons can be biased by a low sampling resolution, patchy distribution, and species misidentification. If properly tested, the correction factor could potentially provide a simple method to estimate the change in *M. ovum* abundance over time, for example, from the preserved monitoring samples. However, this correction factor cannot be proposed as globally accurate for all locations, seasons or species, since specimen recovery is also dependent on other factors such as the physical condition and size of the specimen.

Interestingly, these datasets clearly demonstrate the importance of and demand for good quality sampling with alternative sampling methods and long-term monitoring. To obtain robust abundance

estimates when organisms are patchily distributed, large volumes of water need to be sampled with appropriate equipment (nets and *in situ* methods), and with correct species identification. Raskoff et al. (2003) and Purcell (2009) summarize recommendations for research methods for gelatinous zooplankton, however, some of the methods are too tedious (e.g. three different net types) and expensive (e.g. ROV and In Situ Ichtyoplankton Imaging System [ISIIS]) for regular monitoring programs. Thus, the monitoring of gelatinous plankton communities need to be planned specially on a regional scale to be able to detect the local species compositions, abundances, and potential changes.

4.3. Role of ctenophores in the ecosystem

The focus of the third part of this thesis was in the role of *Mertensia ovum* in the marine ecosystem. The aim of these studies was to describe the predation impact of the Arctic population and how the patchy distribution affects the predation efficiency (**IV**), as well as how the role in the food web might differ from population to population, even within a single species (**V**). Here, the main results of these two articles are presented.

4.3.1. Effects of patchiness on predation impact

Based on previous reports (e.g. Falk-Petersen et al. 2002, Lundberg et al. 2006, Graeve et al. 2008, Purcell et al. 2010), feeding experiments (**IV**), and gut content analyses (for detailed methods, see article **IV**), *M. ovum* in the Arctic has been described to be a voracious predator that mainly preys on *Calanus* spp. (Fig. 8). The functional response experiments resulted in a nonlinear response curve, with an apparent saturation level at higher prey density with a higher ingestion rate than reported earlier (e.g. Swanberg & Båmstedt 1991a, b), suggesting *M. ovum* to be an even more efficient predator than previously believed. Interestingly, neither the ingestion nor the clearance rates declined significantly when predator density was increased in the experiments (see Fig. 4 at article **IV**). It has been thought that tentacle feeders, such as cydippid ctenophores, should exhibit a mechanical limitation when occurring in high aggregations, thus decreasing predation efficiency (Madin 1988). However, no signs of such intraspecific interference were detected, even at predator densities of 500 ind m^{-3}, the highest density used in the experiments. Presumably, the absence of intraspecific competition might be a result of ctenophores adapting to efficient avoidance of tentacle interactions due to frequent encounters in high-density patches.

The data revealed that *M. ovum* may consume an average of 1.4 % d^{-1} of the *Calanus* spp. community in the whole water column when assuming even distributions of predators and prey within the examined depth layer and using the ingestion rates from functional response experiments (Fig. 9). These estimates are similar to those reported in earlier studies, as Siferd and Conover (1992) projected that average-sized *M. ovum* may consume 3 to 9 % of the copepods in the Canadian Arctic per day, and Purcell et al. (2010) estimated that *M. ovum* could remove ~2 % of the *Calanus* spp. standing stock daily. If all predator specimens were detected evenly in the upper 20 m layer, as previously reported from the Arctic, the predation impact would increase rapidly to an average of 33 % d^{-1} of the *Calanus* spp. in this layer. In addition, since ingestion rates

did not significantly decline at high predator aggregations the predation impact increased locally to >50 % d^{-1} when underestimated predator abundances were corrected by taking spatial predator aggregations into consideration (e.g. for details see Table 4 at article **IV**). As the maximum ingestion rate and saturation level were detected at relatively high prey concentrations, the patchy distribution of prey may also increase the predation impact of these predators.

Even though many approximations, such as complete spatial and temporal overlap of the predator and prey patches, were necessary when estimating the predation impact, it was clear that when both predators and prey were assumed to have uneven distributions, the potential predation pressure did not increase consistently with increasing numbers of predators. These results, as well as other predation-impact models that take these aggregations into consideration, indicate that prey patchiness may be advantageous for the predator at high densities, if the predator is able to compensate by implementing non-random searching behavior (Dagg 1977, Arai 1992). Nachman (2006a, b) suggested that such behavior would lead to a response whereby the majority of predators would cluster in the most profitable prey patches, a pattern that can often be observed among *M. ovum* specimens in the Arctic while scuba diving. If the degree of prey density is high, predators may be able to achieve a higher ingestion rate than they would if the prey were homogenously distributed. These results therefore suggest that the potential predation impact of *M. ovum* may even increase significantly with an increased prey density during the summer, when the prey densities in the surface waters are naturally higher than during the time that the experiments were carried out (late summer/autumn). However, the accumulation of prey into high-density patches might also be beneficial to the prey if the density is higher than the saturation level of predator feeding (**IV**, Nachman 2006a, b).

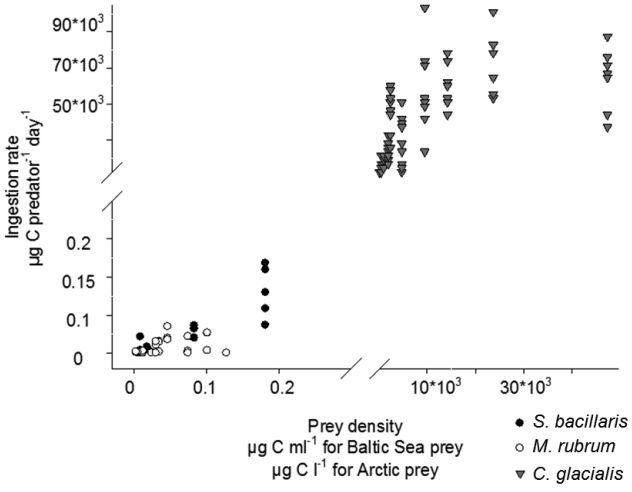


Fig. 8. Ingestion rates of *Mertensia ovum* from the Baltic Sea (*Mesodinium rubrum* and *Synechococcus bacillaris* as a prey) and Arctic (*Calanus glacialis,* stage V, as a prey) determined in experiments as carbon consumed per day. Carbon values 0.00056 µg C ind^{-1} for *M. rubrum* (Johnson et al. 2007), 0.000025 µg C ind^{-1} for *S. bacillaris* (Mullin et al. 1966) and 474 µg C ind^{-1} for *C. glacialis* (Slagstad & Tande 1990).

These findings strengthen the conclusion regarding the importance of understanding spatial patterns when describing such prey–predator interactions (**IV**). In addition, ctenophores may have an important role in Arctic waters, and underestimates due to not considering patchy distributions could lead to inaccurate conclusions, for example, the ability of the predators to regulate their prey densities (Hochberg & Holt 1999). Therefore, it would be more than justified to study further these fine-scale interactions and to include these important predators in multi-trophic datasets as a basis for food-web modeling.

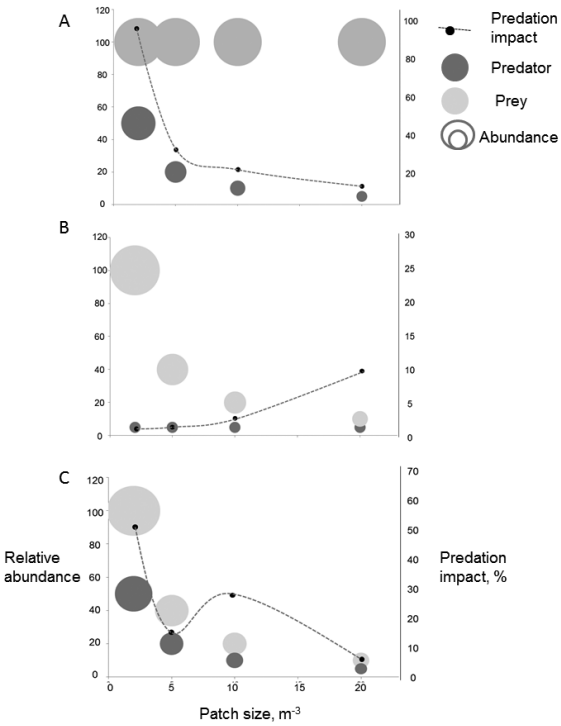


Fig. 9. Schematic figure showing the different uneven spatial distribution models of *Mertensia ovum* (predator) and its prey used in article **IV**. A) Predator in aggregations and prey evenly distributed; B) Prey in aggregations and predator evenly distributed; C) Both predator and prey aggregations. Dark gray is the predator, light gray the prey and the size of the bubble indicates the relative abundance. Predation impact (%) is marked as dotted line.

4.3.2. Predators and grazers

The difference in body size between *M. ovum* populations of the Arctic Ocean and the Baltic Sea is very distinct. In the Baltic Sea, *M. ovum* are small and fragile, as the average size of all specimens collected from different sub-basins was <2 mm (**II**). On the contrary, individual *M. ovum* in the Arctic can grow up to 75 mm (pers. obs.), with an average size of 22 mm (**IV**) (Fig. 3).

In the Baltic Sea (**V**), the average sized *M. ovum* showed clear prey preferences in the experiments. Ingestion and clearance rates for *Eurytemora affinis* copepodites and calanoid copepod nauplii were exceptionally low, also implying significantly lower predation on crustacean prey compared to that shown in other ctenophores in other areas, including *M. ovum* in the Arctic (e.g. **IV**, Kremer 1979, Falk-Petersen et al. 2002, Granhag et al. 2011). In contrast, small-sized bacterio- and microplankton prey (i.e. *Synechococcus bacillaris* and *Mesodinium rubrum*) were consistently preyed upon during the experiments, even at low prey densities. The molecular gut content analysis (for detailed methods, see article **V**) also revealed that field collected ctenophore samples were positive for the presence of *Synechococcus* sp., indicating the importance of picoplankton to the diet of *M. ovum.* Thus, the trophic level of the Baltic *M. ovum* is lower than that of the Arctic populations but the role of the small-sized *M. ovum* in the Arctic is unknown. In addition, estimates also yielded considerably lower *per capita* ingestion rates for Baltic *M. ovum* (Fig. 8)

than for similar-sized ctenophore species, e.g. tentaculate-stage *Mnemiopsis leidyi* (4 mm), when fed a natural assemblage of microplanktonic prey (Sullivan & Gifford 2004, 2007). Here it is important to note that the preliminary results of the carbon content of the Baltic *M. ovum* (6.86 ± 4.4 µg C ind^{-1} for 5.0 ± 0.9 mm sized specimens [unpubl. data]) are also considerably lower than tentaculate-stage *Mnemiopsis leidyi* (18.45 µg C ind^{-1}, C [mg] = 0.0017 length $[mm]^{1.9247}$ [Sullivan & Gifford 2004]).

The body size of both predators and prey are directly linked to predation success (e.g. Scharf et al. 2000). Thus, the relationship between prey and predator size is of great importance in determining the outcome of interactions among species (Scharf et al. 2000). However, body size is not alone in having an effect; prey selection is dependent on the consumer's capability not just to find prey but also to attack, catch, and handle it (Holling 1959, Buskey et al. 1993, Chesney 2005, Kiørboe 2011). The fragile tentacles of the Baltic Sea *M. ovum* stretch only 1–2 times the total body length and possess few branching tentillae (Fig. 4I), while the tentacles of the similar-sized, larval and transitional stages of *M. leidyi* and larger Arctic *M. ovum* (Fig. 4E) may stretch several times the body length and bear several to hundreds of branching tentillae (Reeve et al. 1978, Matsumoto 1991, Sullivan & Gifford 2004, 2007). The fragile structure of the tentacles and tentillae can cause injuries for small-sized *M. ovum* when pulled by escaping copepod prey. This was observed multiple times during experiments and can lower the predation efficiency.

When comparing predation efficiency among different species, it is important to note that the physical conditions (i.e. temperature, salinity) at which feeding experiments are conducted vary greatly. For ctenophores, the conditions generally represent ambient conditions in temperate and tropical waters (e.g. Sullivan & Gifford 2004, 2007, Buecher & Gasser 1998, Greene et al. 1986). Data on the predation efficiency in cold waters and on the effect of temperature on feeding or metabolism in gelatinous organisms are very scarce, but even the few studies conducted (Gyllenberg & Greve 1979, Martinnussen & Båmstedt 2001, Rowshantabari et al. 2012) demonstrate that temperature plays an important role in feeding and clearance rates, the digestion time, and oxygen consumption. Hence, all these physiological processes should be taken into account when comparing predation and daily carbon intake rates of similar species in different environments to understand the comparative physiology of energy demand and consumption. Therefore, it is not evident that the predation impact of *M. ovum* in the Baltic Sea would be lower than that of other similar-sized ctenophores, even though the daily rations would indicate this. Furthermore, the abundances, prey preferences, and predation efficiencies of the smaller individuals of the Arctic *M. ovum* populations are poorly known, with the majority of reports focusing on large-sized ctenophores (>10 mm).

There are serious limitations with the two commonly used methods to investigate prey-predator interactions. In experimental studies, the effects of small aquarium tanks may influence encounter rates and cause predator and prey vulnerability (e.g. Sullivan & Reeve 1982, Larson 1987, Gibbons & Painting 1992, Hansson & Kiørboe 2006, Møller et al. 2010), leading to biased estimates of predation rates. In traditional gut content analysis, it cannot easily be determined whether the micro- and bacterioplankton prey in question have been ingested (see also e.g. Pitt et al. 2009), whereas crustacean prey are clearly visible in the stomach

cavities if eaten. Thus, using both count-based prey depletion estimates in feeding experiments and PCR-based diet analysis is a better combination for estimation of feeding rates on small-sized prey. This is important for ctenophores as they represent a wide variety of morphological differentiation, and a great deal of this appears to be directly linked to specialization for feeding on prey of different size, behavior, and abundance (**Thesis summary**, Haddock 2007).

4.4. Climate change and ctenophores

In the last part of this thesis, the potential effects of predicted future climate changes on *Mertensia ovum* populations in these two ecosystems were examined. The aim of this study was to determine how the two populations of this single species might differ in their response to climate change (**Thesis summary**). The results of this study are presented here as part of the general discussion on the future of ctenophores.

4.4.1. Climate change and Mertensia ovum

It has recently been argued that gelatinous zooplankton would benefit from the future changes in the ecosystem. The impacts of climate change and the ecosystem effects are often discussed on a global scale, even though these effects will occur at local and regional levels. Therefore, it is important to understand the potential effects not just on the species level but also on the regional scale, such as on the population level.

Article **II** emphasized that the occurrence of the *M. ovum* population in the Baltic Sea is clearly regulated by temperature and salinity. Even though *M. ovum* specimens were found at salinities between 5.5 and 16 and at temperatures from 1 to 8.5 °C (Fig. 10), the highest ctenophore abundances were recorded in waters with salinities ≥ 5.5 and temperatures below 7 °C. In the experiments, the survival of *M. ovum* rapidly declined (< 50 %) at lower [5] and higher [14] salinities within the Baltic Sea population (Fig. 10, **Thesis summary**).

In the Baltic Sea, according to climate change models, the volume-averaged water temperature is predicted to increase and the volume-averaged salinity to decrease during the twenty-first century (**Thesis summary**, Meier, Andersson et al. 2012, Meier, Müller-Karulis et al. 2012). The water volume most suitable for the *M. ovum* population (salinity ≥ 5.5, temperature < 7 °C) would decrease according to the HadCM3-A1B and ECHAM5-A1B1, as well as the A1B3 and A2 driven simulations (Fig. 11, **Thesis summary**). When these simulations are combined with earlier reports, where the largest bottom salinity decrease has been found, it is predicted that the current main occurrence area of *M. ovum* in the Baltic Sea would decrease dramatically, even with the most optimistic climate change scenario: from 10–14 × 10^3 km^3 during summer 2013 to 1–8 × 10^3 km^3 by summer 2100, and from 15–20 × 10^3 km^3 during winter 2013 to 1–10 × 10^3 km^3 by winter 2100 (Fig. 11).

In the Arctic, where the effects of the predicted climate change are estimated to be the strongest, *M. ovum* is present in high abundances, primarily in the surface waters (salinity 32–34 and temperature below 5 °C) (Fig. 10, **Thesis summary**). However during the extensive sampling in 2008–2011, it was clear that *M. ovum* can tolerate a broad range of salinity and temperature conditions, as it was found in salinities between 28 and 35, and in temperatures from -1.8 to 7 °C (unpubl. data). In the tolerance experiments,

the survival was stable (100 %) in salinities of 40, 35, and 30, together with the *in situ* salinity level, whereas at lower salinities (< 28), lower survival (< 50 %) was recorded. According to earlier reports, *M. ovum* occurs in areas where the water temperature is constantly below 10 °C (Eiane & Tande 2009) which was also the critical temperature limit for the survival in the experiments; at temperatures >10 °C the survival was < 50 %.

In the Arctic, atmospheric warming has increased sea surface temperature and has led to a decrease in sea ice extent and thickness. In addition, the unprecedented amount of fresh water in the surface layer is predicted to result in warming of the surface layers by up to 3 ºC above average in ice-free areas that previously were ice covered (Wassman et al. 2011 and references therein). According to Beaugrand et al. (2008), the critical thermal boundary (10 ºC) could move northwards as much as 10º in latitude by 2100. Even though the threshold coincides with the maximum upper lethal temperature of *M. ovum,* the changed borderline does not cross the known distributional boundaries for *M. ovum* (Beaugrand et al. 2008 Fig. 2, **Thesis summary**). However, such a fine resolution climate model that was used in the Baltic Sea, is lacking for the surface waters of the Arctic fjords, where *M. ovum* is most abundant during autumn (**Thesis summary**). In the Arctic, the maximal sea surface temperature is measured during autumn, and thus, creates

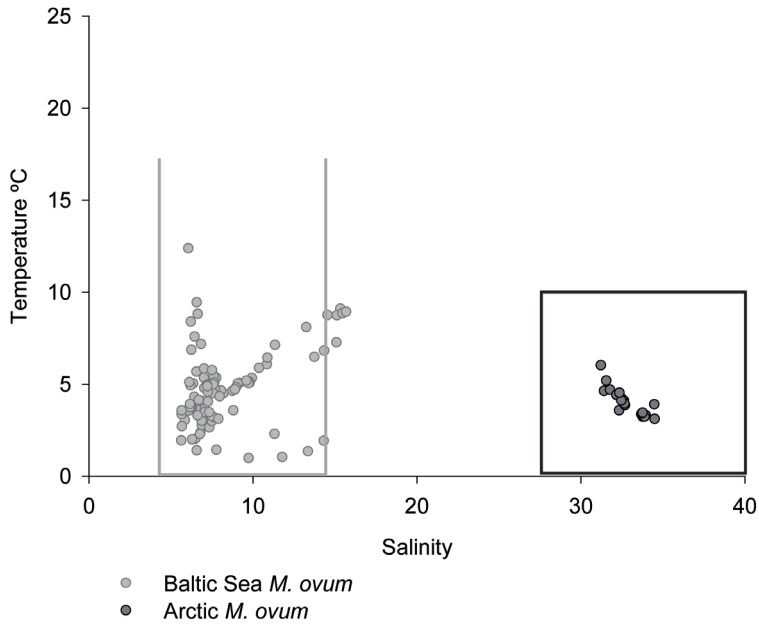


Fig. 10. The salinity and temperature range where *Mertensia ovum* occurs in the Baltic Sea (gray dots) and in the Arctic (black dots) according to *in situ* samples. Note: wintertime samples from the Arctic are not included. The lines show the salinity and temperature tolerance of *M. ovum* populations based on tolerance experiments. Note: the temperature range was not tested with the Baltic Sea population.

a boundary for their survival. In this study, the maximum temperature in the fjords during autumn was 7 °C. Even though future predictions are limited, trends throughout the last century (1912-2009) have indicated an increase of 2ºC of maximum temperature during autumn for Isfjord (Pavlov et al. 2013). Therefore, the critical thermal boundary (10 ºC) could be reached only very locally in the surface in the fjords during autumn, and thus the distribution area of *M. ovum* could be predicted to remain more or less constant in the Arctic.

All species are adapted to a certain range of climatic conditions, outside of which they cannot survive without adaptation period. Changes in the climatic environment therefore force species to either adapt to new conditions or move to areas where suitable conditions exist in order to avoid extinction. Some species have shown considerable adaptive plasticity; for example

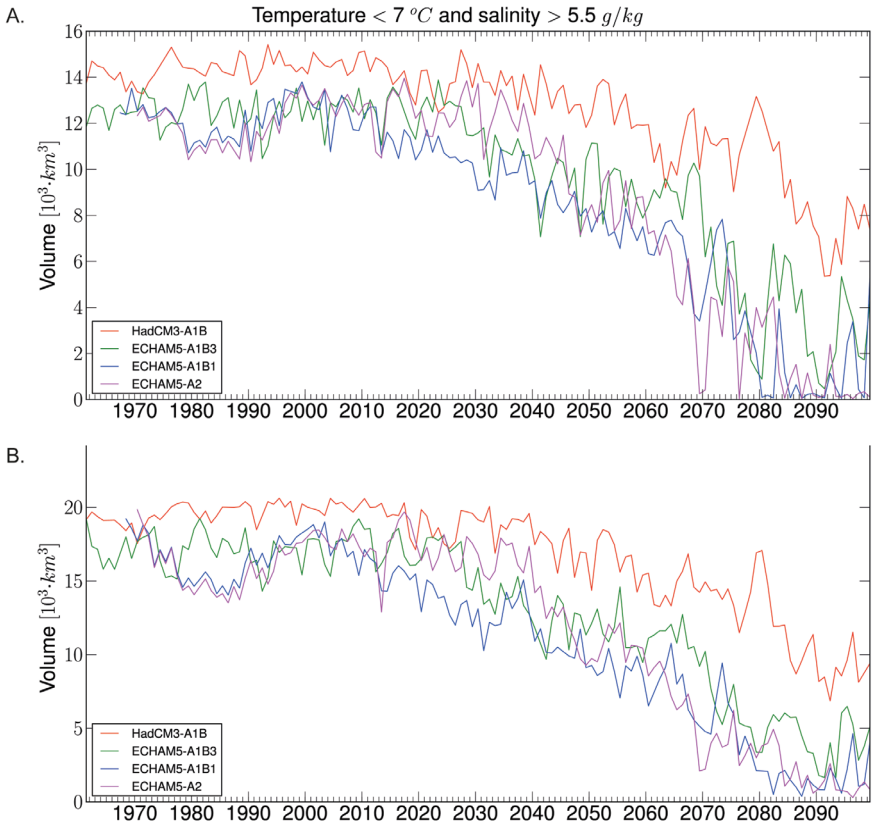


Fig. 11. Future scenarios for the water volume of the current occurrence area of *Mertensia ovum* in the Baltic Sea (temperature < 7ºC and salinity >5.5). A) Represents the situation in summer (June, July and August) and B) the situation in winter (January, February and March). The colors indicate the different predicted climate change scenarios based on IPCC greenhouse gas emission scenarios; A2 being the most pessimistic scenario whereas A1B is more optimistic.

M. leidyi is known to have a wide tolerance of environmental conditions (salinities of 2–38, temperatures between 2 and 32 ºC and low oxygen levels), which enable effective spreading to new areas (Purcell et al. 2001, Fuentes et al. 2010). However, no knowledge exists of the actual evolutionary processes whereby a ctenophore or any other gelatinous zooplankton species becomes adapted to new conditions through changes in its genetic heritage. The recently conducted studies on ctenophore mtDNA and genome indicated that ctenophores evolved independently from the Metazoa for hundreds of millions of years. Therefore, they may have reserved some features from their common ancestor or evolved some unique features not present anywhere else in the animal kingdom (Pett et al. 2011, Kohn et al. 2012, Ryan et al. 2013).

For the Arctic *M. ovum,* its occurrence has been assumed to be more restricted by prey densities than the physical condition of the environment (e.g. Siferd & Conover 1992). Based on earlier reports of SST modeling and the optimal temperatures of the prey species involved (*Calanus* spp.), it has been clear that there will be a shift towards a zooplankton community dominated by *C. finmarchicus* instead of the more energy-rich *C. glacialis* by the end of the 21st century (e.g. Karnovsky et al. 2010). However, it could be assumed that as an opportunistic and voracious feeder, *M. ovum* will be able to adjust its predation and metabolism according to prey availability and therefore also its occurrence area and depth, as it has currently been observed to do throughout the Arctic seasons (see above, Percy 1989, Larson & Harbison 1988, Clarke & Peck 1990). As long as the position of *M. ovum* in the Baltic Sea ecosystem remains open, it can only be speculated whether it has adapted to the demanding brackish water conditions during the last hundred years as an invader, or whether this adaptation evolved during the last 10,000 years as an ice age relict. However, its occurrence is now known to be restricted by the physical conditions (**II**). Thus, adaptation to the changing conditions would be the key to its survival.

Furthermore, studies on adaptive responses are accumulating, and it is speculated that the rate of climate change might be too rapid for adaptation processes to take place (Bürger & Lynch 1995, Gomulkiewicz & Holt 1995, Donner et al. 2005). It is therefore expected that adaptation will be a viable strategy for only a small fraction of species, and that the majority will be forced to shift their distributions in order to survive the forthcoming changes (Parmesan 2006). This view is also supported by evidence from paleoecological records, which suggest that species naturally responded to past climate changes with rapid distribution shifts rather than remaining stationary and adapting to new conditions (Huntley 1991, Coope & Wilkins 1994). Ctenophores are known to have physiological characteristics that are predicted to give them an advantage in changing environmental conditions, and which might make them one of the few taxa able to adapt to changing conditions. For example, features of ctenophore reproductive biology can affect their adaptation potential. In general, they are hermaphrodites capable of self-fertilization (Pianka 1974, Baker & Reeve 1974) and eggs are fertilized when shed (Pang & Martindale 2009). In addition, some ctenophores are capable of rapid reproduction; *M. leidyi* can start reproduction at two weeks of age and release up to 14,000 eggs per day under optimal conditions (Baker & Reeve 1974, Purcell et al. 2001). In the Arctic, the egg production rate is not known, but prolonged reproduction has been observed from May to August (Percy 1989, Siferd & Conover

1992, Lundberg et al. 2006). For *M. ovum* in the Baltic Sea, both eggs sampled *in situ* and egg production experiments indicated extremely low (2.2 ± 1.0 eggs ind^{-1} day^{-1}) but continuous reproduction all year round, potentially limiting the adaptation (for methods and detailed results, see article **II**).

The survival of *M. ovum* is not only dependent on its own adaptation potential because other species or entire plankton communities might experience subtle or distinct regime shifts (e.g. Beaugrand 2004, Hooff & Peterson 2006, Beaugrand et al. 2008). For example, due to changes in salinity and temperature conditions (e.g. Jaspers et al. 2011, Lehtiniemi et al. 2012) and the wide invasion success (reviewed in Purcell et al. 2001, Kideys 2002, Costello et al. 2012), the distribution of *M. leidyi* might spread northwards in the Baltic Sea, causing not only interspecific competition but also potential predation pressure on *M. ovum.* Similarly, new species are expected to shift towards Arctic waters due to climate change and increased shipping activity (e.g. Molnar et al. 2008).

Uncertainty in climate change scenarios is pervasive and will never be entirely eliminated (e.g. Kujala et al. 2012, Niiranen 2013, Niiranen et al. 2013). Uncertainties that arise from working with unknown future events include the technical challenges of observing and predicting species range shifts, and the lack of information on the impacts of future environmental conditions. Reliable monitoring data are also essential when predicting future changes. Currently, abundance data on *M. ovum* in the Arctic are scarce and incoherent, and Baltic Sea data mainly exist from the last 4 years, *i.e.* the period when the occurrence of the species became acknowledged (**II**, **IV**). Thus, it is impossible to exactly consider the changes in abundance in the past or to predict the changes in the future. In addition, for *P. pileus, Euplokamis* sp. and unidentified mertensiids (**I-III**), even their distributions are poorly known (e.g. Mills & Haddock 2007), let alone their abundances. Thus, it is clear that further investigations are required to determine the exact thresholds of physical conditions, prey availability and adaptation potential below which ctenophores will be unable to compensate via phenotypic plasticity and will experience a fitness penalty.

5. CONCLUSIONS

In this thesis, the uncertainties and limitations of the present knowledge of ctenophore biodiversity and their ecological importance were investigated in Svalbard and the Baltic Sea. The main findings from this thesis are that poor taxonomic resolution (both in description and identification of species) is a common problem among the ctenophores, despite their ecological and evolutionary significance (**I–III**), and that inefficient abundance estimates and ignorance of small-scale spatial variability in species distribution can result in erroneous views on ecosystem functioning (**II**, **IV–V**). This thesis clearly demonstrates that without proper monitoring and accurate species identification, it is impossible to assess changes in species distribution and the ecological impact of ctenophores at present or in the future.

Morphology-based species identification showed that in addition to *Mertensia ovum*, at least two other taxa were present in the Arctic samples (**I**). Specimens collected near the entrance of the Baltic Sea also revealed a species new to the area (**III**). However, the few, indistinct morphological

characteristics that were detectable in the collected specimens highlighted the difficulty and challenges in ctenophore identification by different life stages based on morphological features alone. In addition, the lack of accurate species descriptions prevents species-level identification, as can be seen with *Euplokamis* sp. (**I**, **III)** and unidentified mertensiids (**I)**.

When the data sets were analyzed using molecular identification methods, the cydippid ctenophore sequences clustered together with *M. ovum* and *Euplokamis* sp. (sequenced for the first time in article **III**), while some of the sequences were affiliated with an undescribed mertensiid sp. 3 (**I–III**). Based on these studies, it was clear that 18S rDNA and barcoding mtDNA COI regions are not currently suitable markers for ctenophore species identification, whereas the ITS region proved to be more suitable. However, the lack of available sequences with reliable species descriptions and species-specific primers hampers the broad use of molecular methods as a rapid and simple species-identification technique. To better understand the biodiversity of these species in the future, we should apply all available methods, combining taxonomic scrutiny together with photographic vouchers of fresh, live specimens linked to molecular IDs for accurate species identification.

Studies **IV–V** clearly demonstrated that the lack of historical survey data and correct abundance estimates of *M. ovum* hamper our understanding of its role in the Arctic and Baltic ecosystems. The high potential predation impact of *M. ovum* was even higher when the patchiness of both predators and prey was taken into account; moreover, it is further affected by extensive spatial and seasonal migration patterns (**IV**). For adequate modeling of prey–predator interactions, more emphasis should be placed on the patterns of fine-scale distribution of predators and prey. Also, the different populations of a single species can have very different trophic roles in the food web due to their great difference in body size (**IV–V**). Thus, generalizing and extrapolating ecological traits such as diet and foraging behavior from one population to another can be misleading (**V**). Caution is advised when studies and monitoring are conducted at different regional scales.

The overall conclusion is that all available techniques need to be applied in concert to include ctenophores, as well as other gelatinous zooplankton, in the regular plankton monitoring in order to properly understand their role and potential future changes in the planktonic communities. Current monitoring of plankton is mostly focused on crustaceans and fish larvae, without proper consideration of the gelatinous component, which is as incomplete as a hypothetical ecological study of the Serengeti through observations of zebras and hyenas only. This would surely lead to inadequate conclusions, as it would ignore not only cheetahs (ctenophores) but also lions (cnidarians) (Boero & Mills 1997). Even though this demand has already been acknowledged (e.g. Condon et al. 2012, Brotz et al. 2012, Gibbons & Richardson 2013), clear recommendations and instructions for a proper assessment of gelatinous zooplankton taxa implementation in monitoring are urgently needed as well as more ecological and phylogenetic research on this group.

6. IMPLICATIONS AND FUTURE DIRECTIONS

It has been widely accepted that climate change is altering ecosystems and species distributions (e.g. reviewed for the Arctic in Wassmann et al. 2011). However, observations on certain species, especially ctenophores and other gelatinous zooplankton, are lagging behind (**Thesis summary**, Condon et al. 2012, Gibbons & Richardson 2013).

Comprehensive and accurate information on these species from surveys and monitoring at different scales is essential if we want to 1) know the current situation, 2) understand the ongoing changes, 3) anticipate future impacts, and 4) potentially be able to rapidly react to the threats posed by climate change. In the case of species for which identification, abundance estimates, and predictions of future impacts have high uncertainty, intensive monitoring programs might provide the only means for better understanding.

In an ideal world, the first step for efficient monitoring would be to develop accurate species identification methods, with proper morphological species descriptions combined with photographic vouchers, molecular protocols and reference sequences of specimens. A second important step would be the development of data collection techniques to include small-scale distribution patterns. In addition, national population monitoring programs should be further developed to ensure collecting and reporting monitoring data for these species. At the moment, this is vital in the Baltic Sea, where the regional monitoring program is under revision and in the Arctic, where the Circumpolar Biodiversity Monitoring Program (CBMP) is currently working to harmonize and enhance long-term marine monitoring efforts.

This work offers tools to assist in robust research and decision making when ctenophore biodiversity and their role in marine ecosystems need to be assessed. Many of the chapters in the thesis summary demonstrate how better knowledge can be acquired by combining information from several data sources and using different methodologies. Furthermore, this thesis summary provides useful information for managers on the important role of ctenophores in ecosystems and the challenges of ctenophore research that can be and should be overcome by long-term monitoring, planning, and ecosystem modeling.

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