Studies on dinoflagellates in the northern Baltic Sea

HEIDI HÄLLFORS

This thesis is based on the following studies, which are referred to by their Roman numerals:

I.   **Hällfors, H.**, Backer, H., Leppänen, J.-M., Hällfors, S., Hällfors, G. & Kuosa, H. 2013: The northern Baltic Sea phytoplankton communities in 1903–1911 and 1993–2005: a comparison of historical and modern species data. – Hydrobiologia, in press, DOI 10.1007/s10750-012-1414-4.

II.   **Hällfors, H.**, Hällfors, S., Kuosa, H. & Olsonen, R.: Seasonal and interannual occurrence of dinoflagellates in the northern Baltic proper and the western Gulf of Finland in 1993–2000. – Manuscript.

III.   Rintala, J.-M., **Hällfors, H.**, Hällfors, S., Hällfors, G., Majaneva, M. & Blomster, J. 2010: *Heterocapsa arctica* subsp. *frigida* subsp. nov. (Peridiniales, Dinophyceae) – description of a new dinoflagellate and its occurrence in the Baltic Sea. – Journal of Phycology 46(4):751–762.

IV.   **Hällfors, H.**, Hajdu, S., Kuosa, H. & Larsson, U. 2011: Vertical and temporal distribution of the dinoflagellates *Dinophysis acuminata* and *D. norvegica* in the Baltic Sea. – Boreal Environment Research 16(2):121–135.

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The authors' contributions to the articles

	Study I	Study II	Study III	Study IV
Original idea	HH, GH, SeH	SeH, GH	GH, SeH, JMR	HH, SuH, HK
Microscopy (LM, Epi, EM)	SeH, HH, MH, KML[1], YW[1]	SeH, MH	SeH, JMR, GH, HH, MH	SuH, HH
Processing of phytoplankton count data	HH	HH	HH	HH, SuH
Culturing	-	-	JMR	-
Phylogenetic analysis	-	-	JB, MM	-
Statistical analysis	HB, HH, HK	HH, RO	MM	HK
Responsible for ms	HH	HH	JMR, HH	HH
Contributions to ms (text, figures, comments)	HB, HK, SeH, GH, JML	HK, SeH, RO	MM, JB, SeH, GH	SuH, HK, UL

[1] historical data

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STUDIES ON DINOFLAGELLATES IN THE NORTHERN BALTIC SEA

HEIDI HÄLLFORS

Dinoflagellates are an important part of the Baltic Sea phytoplankton community. The group includes significant primary producers, consumers, bloom-forming species, toxic species, and species capable of rapid expansion to new areas. The aim of this thesis is to provide new information on the occurrence of dinoflagellates in the northern Baltic proper and the western Gulf of Finland by investigating 1) trends in temporal and spatial distribution of dinoflagellates, 2) patterns of co-occurring taxa in the dinoflagellate community, and 3) external factors that explain dinoflagellate occurrence.

These issues were investigated in four studies, on which this thesis is based. In the first study, we compared the phytoplankton communities of the early 1900s and the present, and examined the role of dinoflagellates in the species compositions of these two periods. In the second study, the focal point was moved forward in time to the annual and interannual dynamics and diversity of the present-day dinoflagellate community, and in the third study further to a more detailed level, the description of a new taxon, *Heterocapsa arctica* subsp. *frigida*, and its ecology and distribution. Lastly, in the fourth study we shifted focus from seasonal, interannual and geographical occurrence to smaller-scale occurrence, i.e. the vertical distribution of dinoflagellates in the water column, as represented by a case study on *Dinophysis acuminata* and *D. norvegica*.

A total of 47 dinoflagellate species, 28 genera, and four higher-level taxa were observed. Of the species-level taxa, 15 have not been previously reported from the northern Baltic proper and/or the Gulf of Finland. We also contributed to the knowledge of Baltic Sea dinoflagellate diversity by formally describing the new taxon, *Heterocapsa arctica* subsp. *frigida*, which furthermore represents a for phytoplankton unusual taxonomical level, i.e. a subspecies. The conspecificity of *H. arctica* subsp. *frigida* with *H. arctica* subsp. *arctica*, described from the Canadian Arctic, was demonstrated by their practically identical ITS rDNA sequences in combination with similarities in the morphological characteristics which are important in distinguishing between members of the genus *Heterocapsa* (i.e. body scale structure, shape and position of the nucleus, and position and ultrastructure of the pyrenoid). Despite the aforementioned similarities in genotype and fine structure, the two dinoflagellates can easily be distinguished by their general morphology; this together with their distinct geographical distributions warranted the description of the new subspecies.

Investigating a selection of taxa comprising dinoflagellates, diatoms, cyanophytes, a chrysophyte and a chlorophyte, we documented clear differences in the historical (1903–1911) and modern (1993–2005) phytoplankton communities. The most obvious differences were the increased occurrence of dinoflagellates and the decrease in the diatom to dinoflagellate ratio in all seasons. Focusing on the present-day dinoflagellate community (1993–2000), we

found a change in species composition even within the relatively short 8-year study period. None of the examined environmental descriptors could explain the observed centurial or decadal shifts. In light of the severe eutrophication of the Baltic Sea during the 20th century and the documented sensitivity of phytoplankton to different nutrient levels, we are inclined to interpret the centurial shift in phytoplankton communities as evidence of the direct and/ or indirect influence of nutrient enrichment, though we lack data on the nutrient status a century ago. An attempt to find eutrophication indicator species failed, however, since none of the 10 candidate taxa fulfilled the criteria of good indicator species.

On an annual scale, temperature in combination with season is the best predictor of dinoflagellate species composition. The dinoflagellates formed five groups according to their seasonality: vernal, early summer, summer and autumn, throughout the growing season occurring, and generalist taxa; sporadically occurring dinoflagellates constituted a sixth group. The seasonal groups reflect the annual succession from dinoflagellates occurring in a high-biomass spring bloom community that thrives in cold, nutrient-rich waters, to dinoflagellates occurring later in the year in warm, nutrient-poor waters with a lower phytoplankton biomass. Overall, annual succession is of much greater importance than interannual variability in explaining variation in the dinoflagellate species composition in the northern Baltic Sea.

Their regular presence and tendency to form subsurface maxima qualified *Dinophysis acuminata* and *D. norvegica* as suitable case study objects to investigate the vertical distribution patterns of dinoflagellates. Both species formed population maxima either in the nutrient-poor mixed surface layer above 10 m depth, or alternatively, below 10 m depth, in or out of the euphotic zone but near the thermocline and coinciding with a nutricline. When *D. acuminata* and *D. norvegica* co-occurred, their abundances peaked at different depths, even when both species formed maxima in the surface layer. This emphasizes the importance of accurate species determinations and the riskiness of drawing conclusions on the ecology of one species based on findings regarding a close relative. Based on our results, the primary mode of nutrition for *D. acuminata* in the northern Baltic Sea seems to be photoautotrophy, and also *D. norvegica* may utilize photoautotrophy to a greater extent than lately suggested.

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CONTENTS

1. INTRODUCTION

Dinoflagellates are a diverse and versatile group of microscopic organisms. The names used for the taxonomical division of dinoflagellates, Dinophyta and Pyrrhophyta, come from the Greek; *dino* referring to the characteristic whirling movement of the organisms, *pyrrhos* meaning flame-coloured (Spector 1984, Dodge 1985). The approximately 2 000 extant species described worldwide have successfully adapted to a wide variety of pelagic and benthic habitats encompassing everything from arctic and tropical seas to freshwaters and brackish-water estuaries, hypersaline waters, sea ice and even snow (Taylor 1987a, 1987b, Steidinger & Tangen 1996). In any aquatic ecosystem, there hardly exists an environmental condition not exploited by dinoflagellates (Smayda 2002). From the Baltic Sea, over 200 dinoflagellate species in 50 genera have been recorded (G. Hällfors 2004). About one third of these species occur in the northern Baltic proper and the Gulf of Finland (G. Hällfors 2004), the areas investigated within the framework of this thesis.

1.1. Why study dinoflagellates?

In the northern Baltic Sea, dinoflagellates are an important part of the pelagic ecosystem. The group constitutes important primary producers (cf. Bruun et al. 1980, Piippola & Kononen 1995) and consumers (cf. Hansen 1991, Bralewska & Witek 1995), bloom-forming species (Lindholm & Nummelin 1999, Jaanus et al. 2006), toxin-producing species (Edler et al. 1996, Uronen 2007) and species capable of rapid expansion to new areas (Hajdu et al. 2000, Olenina et al. 2010). Dinoflagellates are ubiquitous and abundant; they are present throughout the growing season (cf. Kononen & Niemi 1984, 1986) and even in and under the sea ice (Huttunen & Niemi 1986, Ikävalko & Thomsen 1997). Dinoflagellates, even single species, commonly make up 50–95 % of the total (nano- and micro-sized) phytoplankton biomass, particularly during spring but also in summer (e.g. Niemi 1975, Gasiūnaitė et al. 2005, Jaanus et al. 2011).

1.1.1. Dinoflagellates as primary producers and consumers

Commonly the term *phytoplankton*, meaning the microscopic primary producers of the pelagic ecosystem, is applied to dinoflagellates although in view of their nutrition the term *protist*, encompassing as it does heterotrophic organisms also, would be more accurate. About half of the species are photosynthetic, half are obligate heterotrophs, i.e. they lack chloroplasts and live exclusively on organic matter (Gaines & Elbrächter 1987). Consumption of particulate organic matter in the form of phytoplankton or protist prey has been demonstrated (e.g. Jacobson & Anderson 1986, Hansen 1992), but the mechanism through which dissolved organic matter stimulates dinoflagellate growth is not yet fully clear (Granéli et al. 1985, 1999, Purina et al. 2004, Fagerberg et al. 2009). The nutrition of the group is very complicated; many of the chloroplast-bearing dinoflagellates are mixotrophs, functioning both as producers and consumers (Stoecker 1999, Hansen 2011). Moreover, some dinoflagellates apparently possess kleptoplastids, from other organisms through ingestion "stolen" chloroplasts (e.g. Janson 2004, Minnhagen 2010), although the concept is currently disputed, and they may in fact represent temporary endosymbiosis (Hansen

2011). Very few dinoflagellates are strict autotrophs; most photosynthetic species are auxotrophic, requiring organic compounds such as vitamins for their cell functions (Gaines & Elbrächter 1987, Tang et al. 2010). In this thesis, the term *autotrophic* is used in the broad sense, meaning chloroplast-bearing, irrespective of chloroplast origin or degree of mixotrophy.

Traditionally, both autotrophic and heterotrophic dinoflagellates have been counted in phytoplankton analyses. So far, most research has focused on the dinoflagellates' role as primary producers (cf. Taylor 1987a, 1987b), the importance of which is well established. A less well-recognized fact is that heterotrophic dinoflagellates constitute a significant part of the biomass of microplanktic consumers (reviewed by Sherr & Sherr 2007). In fact, they are often more abundant than ciliates, traditionally considered the most important protist herbivores. In both oligotrophic and eutrophic pelagic systems, heterotrophic microplankton are quantitatively more important grazers of phytoplankton than even the mesozooplankton, larger-sized consumers that include groups such as copepods (Sherr & Sherr 2007 and references therein). The significance of heterotrophic (or chloroplast-bearing, but predatory) dinoflagellates in the northern Baltic Sea food web has not been extensively investigated, but taxa commonly occurring in the area have been studied in the south(west)ern Baltic Sea (Smetacek 1981, Hansen 1991, Bralewska & Witek 1995) and elsewhere (cf. Jeong et al. 2004, Sherr & Sherr 2007, Hansen 2011), and their importance has been unequivocally demonstrated. Many heterotrophic dinoflagellates are voracious predators, consuming prey as large as themselves or even larger (e.g. Jacobson & Anderson 1986, Hansen 1992, Jeong et al. 2004).

Due to the complex nutrition of many dinoflagellates (cf. Minnhagen et al. 2008, Garcia-Cuetos et al. 2010, Hansen 2011), many details of their ecology are as yet largely unresolved. The nutritional diversity and flexibility of dinoflagellates very probably contribute to the success of the group.

1.1.2. Dinoflagellate blooms, toxicity and invasive species

When occurring in high abundance, dinoflagellates discolour the water in various shades of reddish-brown; hence dinoflagellate blooms are called red tides. Bloom-forming species are virtually always photosynthetic; only few heterotrophic dinoflagellates occur in high abundances (Larsen & Sournia 1991). In the northern Baltic Sea, dinoflagellate blooms are an annual phenomenon in spring (cf. Kremp 2000, Jaanus et al. 2006, Klais et al. 2011), and common in summer also (cf. Rantajärvi 1995, 1996, 1997, 1998). Some of these bloom-formers produce toxins, e.g. *Alexandrium ostenfeldii* (Kremp et al. 2009, Hakanen et al. 2012) and *Dinophysis* spp. (Kuuppo et al. 2006, Setälä et al. 2009); however, thus far no harmful effects of dinoflagellates on humans have been reported from the northern Baltic Sea.

In a global perspective, the consumption of shellfish is one of the most important pathways via which dinoflagellate toxins affect humans (cf. Hallegraeff 2003). Since cultivation of shellfish for human consumption is restricted to the Kattegat region in the southwestern Baltic Sea, dinoflagellate toxicity has until recently received little attention in the northern sea areas. Here, diarrhoetic shellfish poisoning (DSP) toxins have been found in water samples containing *Dinophysis* species, as well as in copepod faecal pellets (Kuuppo

et al. 2006), copepods (Setälä et al. 2009), blue mussels (Pimiä et al. 1997), and flounder (Sipiä et al. 2000), a fish species that feeds on blue mussels. Paralytic shellfish poisoning (PSP) toxins produced by *Alexandrium ostenfeldii* (Kremp et al. 2009, Hakanen et al. 2012) have been found in bivalves (Hakanen et al. 2012 citing Setälä et al. unpublished data) and copepods (Sopanen et al. 2011). Even in cases in which no toxins were found in the zooplankton itself, *A. ostenfeldii* and its exudates had an incapacitating, even lethal, effect on the copepods (Sopanen et al. 2011). Thus, although not constituting an acute threat to human health in the northern Baltic Sea, toxic dinoflagellates are a potential risk for co-occurring organisms, as well as for high-trophic-level consumers, through toxin bioaccumulation in the food web (cf. Kuuppo et al. 2006, Setälä et al. 2009, Hakanen et al. 2012; but see Setälä et al. 2011).

Whether through natural range expansion, or assisted by man, e.g. through ballast water exchange or the transfer of cultivated shellfish, dinoflagellates have the capacity to invade new areas (Hallegraeff & Bolch 1992, Honjo et al. 1998, Smayda 2002). A well-known recent introduction in the northern Baltic Sea is *Prorocentrum minimum* (Hajdu et al. 2000, Olenina et al. 2010). This species was first observed in the southern Baltic Sea in the early 1980s, from where it subsequently expanded northward, and was found for the first time in the Gulf of Finland a decade later (Hajdu et al. 2000 and references therein). *Dinophysis acuta* is apparently another fairly recent newcomer to the northern Baltic Sea; it may have expanded into this area as recently as the late 1980s–early 1990s (Edler et al. 1996). Both species show signs of being established members of the northern Baltic Sea phytoplankton community (Olenina et al. 2010, studies I–II).

1.1.3. Motility and the benefits of forming layers

Being flagellated and therefore motile, dinoflagellates have the potential to regulate their position in the water column (Raven & Richardson 1984, Edler & Olsson 1985, Olli et al. 1998). In the Baltic Sea, where the surface waters are temperature-stratified for most of the growing season, motility is a feature of great ecological significance. Their ability to swim hinders dinoflagellates from sinking and facilitates the seeking out of optimal growth conditions (e.g. Smayda 2002). Photosynthetic dinoflagellates can thus exploit both the illuminated, but nutrient-depleted, surface layer and the deeper nutrient-rich waters, giving them an advantage over the non-motile planktic diatoms, worldwide the dinoflagellates' foremost rivals among primary producers (e.g. Rines et al. 2010). For heterotrophic and mixotrophic dinoflagellates, motility enables the seeking out of prey populations or layers with other suitable organic substrates (e.g. Smayda 2002).

Impressive swimming velocities of several metres per hour have been measured for dinoflagellates (Levandowski & Kaneta 1987, Spilling 2001, Jeong et al. 2004). Many (possibly even most) dinoflagellates migrate up and down in the water column on a daily basis; these vertically migrating populations typically swim towards the surface in the morning and downwards in the evening (Levandowski & Kaneta 1987, Taylor 1987b). However, in the Baltic Sea, prolonged, non-diel vertical migration has been observed in *Heterocapsa triquetra* (Kononen et al. 2003) and proposed for *Dinophysis acuminata* (Setälä et al. 2005).

Many dinoflagellates aggregate at particular depths (Kuosa 1990, Lindholm 1992, Kononen et al. 2003, Hajdu et

al. 2007). In addition to attaining better nutritional conditions, suggested reasons for layer-forming include avoidance of high irradiances, as well as unsuitable salinity or temperature conditions (Taylor 1987b, Passow 1991, Carpenter et al. 1995). Further reasons for layer-forming include the benefits gained from occurring in dense populations. At high cell densities, a population may chemically modify the local environment so that potential chemical defences become effective at reducing losses through grazing and at deterring competitors through allelopathic effects (Donaghay & Osborn 1997, Rines et al. 2010). Lindahl et al. (2007) found a negative correlation between *D. acuminata* population density and toxicity per cell, suggesting that to reach toxin levels which produce an allelopathic effect, *D. acuminata* individuals in low-density populations must produce more toxins than those in denser populations. Assuming that the toxins are not a metabolical by-product and therefore are energy-consuming to produce, individuals in high-density populations would thus benefit from having to delegate fewer resources to maintaining chemical defences (Lindahl et al. 2007). A concentrated population, safeguarded by chemical defences, would also serve as a refuge for a large vegetative seed stock lying low during unfavourable conditions (Donaghay & Osborn 1997). Finally, chemical signals may also attract reproductively compatible individuals, which would ensure the release of sufficient gametes for successful mating (Donaghay & Osborn 1997, Reguera 2002). This has been suggested e.g. for *Dinophysis* species: vertical aggregation appears to trigger an increase in individuals and the formation of small cells, which may be associated with the sexual cycle (Reguera 2002).

Thus it appears self-evident that protists capable of controlling their position in the water column will form layers. Whether they persist at a particular depth or perform migration probably varies, depending on the causes initiating the forming of layers.

2.   AIMS AND SCOPE OF THIS THESIS

This thesis had three main objectives, namely 1) to reveal trends in the temporal and spatial distribution of dinoflagellates, 2) to uncover patterns of co-occurring taxa in the dinoflagellate community, and 3) to discover which external factors predict the occurrence of dinoflagellate taxa, in the northern Baltic Sea.

These issues were investigated through four studies. In study I, we compared the phytoplankton communities of the early 1900s and today, and examined the role of dinoflagellates in the species compositions of these two periods. In studies II–III, the focal point was moved forward in time to the annual and interannual dynamics and diversity of the present-day dinoflagellate community (study II), and further to a more detailed level, the description of a new taxon and its ecology and distribution (study III). Lastly, in study IV we shifted focus from seasonal, interannual and geographical occurrence to smaller-scale occurrence, i.e. the vertical distribution of dinoflagellates in the water column. Here, I review our main findings and discuss the use of some less commonly applied materials and methods.

3.   THE BALTIC SEA

3.1.   General features

The Baltic Sea is a young sea that evolved into its present form after the withdrawal of ice at the end of the last glaciation c. 10 000 years ago (Winterhalter et al. 1981, Björck 1995). Today the Baltic Sea, extending over some 1 300 km between the 54°N and 66°N latitudes in northern Europe, is a semi-enclosed, practically non-tidal, brackish-water estuary with great horizontal, vertical and seasonal variations in its physical, chemical and biological characteristics. The surface water temperature varies from about 15–20° C in late summer to freezing in winter, the northernmost areas being ice-covered for several months (Voipio 1981, Wulff et al. 2001). The surface water salinity decreases from 15–25 (PSU, Practical Salinity Units) in the Kattegat to below 3 in the eastern Gulf of Finland and the northern Gulf of Bothnia (Voipio 1981, Wulff et al. 2001), hence the biota is a mixture of marine and freshwater species (G. Hällfors et al. 1981).

The influence of salinity in structuring the phytoplankton community is evident, both on the aforementioned south-to-north gradient (Gasiūnaitė et al. 2005, Olli et al. 2011) and on an offshore-to-inshore gradient (Niemi 1973). The general pattern of phytoplankton annual succession follows climatic conditions (Niemi 1975), which differ with latitude. Consequently, both phytoplankton community composition and annual succession differ in the southern and northern sea areas (cf. G. Hällfors et al. 1981, Wasmund & Siegel 2008, Jaanus et al. 2011).

3.2.   Study area

To explore differences in the dinoflagellate community beyond the geographical, a study area in the open northern Baltic proper and western Gulf of Finland with similar prevailing environmental conditions and similar timing of the seasonal phytoplankton succession was selected. Here, the surface water salinity is usually in the range of 4.5–7.5 (studies I–II, IV). There is no natural border between the two sea areas; the Gulf of Finland is a direct extension of the Baltic proper. Following G. Hällfors (2004), the boundary between the northern Baltic proper and the Gulf of Finland runs along the 23°E longitude, and the northern Baltic proper is delimited by the 59°45'N and the 58°N latitudes. The eastern border of the study area was at approximately the 25°E longitude, at Helsinki, Finland. Only in study III, in which the distribution of a new dinoflagellate taxon was investigated, the study area extends outside this main study area, through the central and southern Baltic proper all the way to the Mecklenburg Bight. The bulk of the data in all four studies was collected in open-sea areas, with the exception of a few samplings closer to shore.

3.3.   The Baltic Sea today and one hundred years ago

The Baltic Sea is one of the most nutrient-enriched seas in the world; it is so severely eutrophied that no unaffected areas remain today (HELCOM 2009a). Man-induced eutrophication is no new phenomenon; it is the oldest environmental problem caused by civilization (Wassmann & Olli 2004), and the Baltic Sea has likely been subject to enhanced nutrient inputs since agriculture and the use of forests began in the area some 5 000

years ago (Odén 1980, Wassmann 2004). There is evidence of eutrophication-related changes, such as hypoxia and shifts in species composition, attributable to considerable nutrient leakage as a consequence of deforestation and agriculture going back almost 2 000 years (Zillén & Conley 2010, see also Weckström 2006).

In the late 19th century, rapid urbanization and industrialization led to a drastic increase in nutrient inputs in some coastal areas (Odén 1980, Billen et al. 1999, Laakkonen & Lehtonen 1999). The historical data investigated within the framework of this thesis (study I) are from the first and second decades of the 20th century. At that time, the two largest cities on the shores of our study area, Helsinki and Stockholm, already had populations of about 130 000 and 300 000, respectively (Finni et al. 2001b, Olsson 2001). In Helsinki alone, almost 200 large industrial facilities were active (Kovero 1955). Wastewater treatment was nonexistent, waste was simply discharged into the sea and consequently the urban near-shore waters of these cities were distinctly eutrophied (Finni et al. 2001b, Johansson & Wallström 2001), some areas even being in worse condition than they are today (cf. Finni et al. 2001b). In the bays of Helsinki, heavy cyanophyte blooms were annually recurring phenomena (Levander 1908, 1913; and references therein), which already at the time were attributed to municipal wastewater and industrial discharges (Finni et al. 2001b, Laakkonen & Laurila 2007; and references therein).

There are no contemporary reports of whether non-urban coastal waters or the open sea were similarly affected by nutrient inputs already during the early 1900s; the current consensus is that on the grand scale of things, man had little eutrophying effect on the Baltic Sea one hundred years ago (e.g. Larsson et al. 1985, Jansson & Dahlberg 1999,

Schernewski & Neumann 2005, Österblom et al. 2007, Nausch et al. 2008, HELCOM 2011a). However, during the course of the 20th century, distinct biological effects attributable to eutrophication emerged. In the northern Baltic proper and the Gulf of Finland, Secchi measurement data show that summertime water transparency in the open sea has decreased by several metres since the early 1900s (Sandén & Håkansson 1996, Fleming-Lehtinen & Kaartokallio 2009). Since the 1940s, this reduced light penetration has affected the flora of rural coastal sites, causing changes in the species composition of diatoms (Weckström 2006, Weckström et al. 2007), and a decreased depth distribution of bladder wrack *Fucus vesiculosus* (Kautsky et al. 1986). All the aforementioned studies concluded that the main cause for the increased water turbidity was an increase in phytoplankton biomass (Kautsky et al. 1986, Sandén & Håkansson 1996, Weckström 2006, Weckström et al. 2007, Fleming-Lehtinen and Kaartokallio 2009). This interpretation is supported by evidence from CO_2 partial pressure calculations (Schneider & Kuss 2004) and reconstructed historical nutrient concentrations (Savchuk et al. 2008), which indicate that phytoplankton primary production has since the early 1900s increased approximately threefold in the Baltic proper, and even more in the Gulf of Finland. In line with this, a comparison of old and new sediment data from the open Baltic proper showed a more than 1.7-fold increase in organic matter deposition between the late 1920s and the late 1980s (Jonsson & Carman 1994). Investigations of stable nitrogen and carbon isotope composition as well as organic carbon content of sediments have subsequently pinpointed the start of the drastic increase in nutrients and productivity to the 1950s–1960s (Andrén et al. 2000, Struck et al. 2000, Poutanen & Nikkilä

2001). This increase is verified by real-time water column measurements; in both the open northern Baltic proper and the Gulf of Finland, wintertime nutrient concentrations and summertime phytoplankton biomass were distinctly lower when the measurements started in the 1950s (phosphate), mid-1960s (nitrite+nitrate), and the 1970s (chlorophyll *a*), than they are today (Fleming-Lehtinen et al. 2008).

Nutrient concentrations increased up to the 1980s in all Baltic Sea areas (HELCOM 2009a). During the 1990s and 2000s, nitrogen and phosphorus levels (both dissolved inorganic fractions and the total nitrogen and total phosphorus concentrations) in surface waters levelled off or decreased in the Baltic proper, but the situation has not improved in the Gulf of Finland (Suikkanen et al. 2007, Fleming-Lehtinen et al. 2008, HELCOM 2009a). Summertime chlorophyll *a* values increased from the 1980s to the mid-2000s in both the northern Baltic proper and the Gulf of Finland (Raateoja et al. 2005, Suikkanen et al. 2007, Fleming-Lehtinen et al. 2008).

Although there is a long tradition of phytoplankton research in the Baltic Sea, the oldest phytoplankton community investigations originate from the late 1800s to the early 1900s (see references in Finni et al. 2001a, G. Hällfors 2004, Heiskanen et al. 2005, Wasmund et al. 2008, study I). Thus no records of the truly pristine Baltic Sea phytoplankton community exist, and we were forced to delimit the temporal span of our centurial study (study I) to cover a period of time when the Baltic Sea was already to some degree influenced by agriculture, industrialization and urbanization. However, based on what we today know of the development in the area, it is safe to say that eutrophication in the open northern Baltic Sea in the early 1900s was not the problem it is today.

4.   MATERIALS AND METHODS

The phytoplankton methodology utilized within the framework of this thesis consists mostly of modern conventional methods (studies I–IV, this thesis). All the data and methods are summarized in Table 1. For the purposes of this thesis, some approaches not commonly used in phytoplankton research were required. These included the comparison of historical and modern phytoplankton species data, semi-quantitative abundance estimations, and the utilization of monitoring data for investigating dinoflagellate diversity. For clarity, these will be discussed below.

4.1.   Comparing historical and modern phytoplankton data (study I)

The comparison of historical and present-day phytoplankton data is notoriously challenging. This is in part due to the limited spatial and/or temporal coverage of most historical studies, in part due to methodological differences (cf. Finni et al. 2001a, Heiskanen et al. 2005, Wasmund et al. 2008, study I). Also, considerable taxonomical knowledge is required for the laborious assessment of the species data and the updating of the nomenclature.

4.1.1. Spatial and temporal coverage of the historical data

The historical data utilized in this thesis (study I) were gathered in the early 1900s on quarterly cruises coordinated by the International Council for the Exploration of the Sea (ICES). This sampling campaign constituted the first internationally coordinated monitoring programme for the Baltic Sea and neighbouring sea areas (Francke 1986). The investigation covered

Table 1. Summary of phytoplankton data and methods utilized. LM, light microscopy; Epi, epifluorescence microscopy; SEM, scanning electron microscopy; TEM, transmission electron microscopy.

	Study I	Study II	Study III	Study IV	This thesis A	This thesis B
Study area	Northern Baltic proper – western Gulf of Finland	Northern Baltic proper – western Gulf of Finland	Southern Baltic Sea – western Gulf of Finland	Northern Baltic proper – western Gulf of Finland	Northern Baltic proper – western Gulf of Finland	Northern Baltic proper – western Gulf of Finland [a]
Study period	1903–1911, 1993–2005	1993–2000	1970s, 1993–2005	1999, 2000, 2004	2001–2005	2004, 2005
Temporal coverage	Spring, summer, autumn	Spring–autumn	All seasons	Spring–autumn	Spring–autumn	Summer
Data resource	ICES [b], Algaline [c]	Algaline [c]	Authors' data, Algaline [c]	Authors' data	Algaline [c, d]	Author's data
Number of samples	1173 (1107 with full environmental data)	932 (602 with full environmental data)	2764 + cultures	299 (23 verticals)	396	130 (9 verticals)
Abundance data	Semi-quantitative [e], used as presence/absence	Semi-quantitative [f]	Semi-quantitative [f]	Quantitative [g]	Semi-quantitative [f]	Semi-quantitative [f], select taxa quantitative [g]
Sample type	Net [h], water [i]	Water [i]	Ice, water [i]	Water [i]	Water [i]	Water [i]
Sampled depth	Integrated surface layer (represents top ~ 20 m)	Integrated surface layer (represents top ~ 20 m)	Integrated surface layer (represents top ~ 20 m)	Discrete samples at 1.0–2.5 m intervals (covering 0–20 or 0–25 m)	Integrated surface layer (represents top ~ 20 m)	Discrete samples at 1.0–2.0 m intervals (covering 0–20 m)
Microscopy	LM	LM	LM, Epi, SEM, TEM	LM	LM	LM
Culture work, experiments	-	-	Effect of salinity on cell size	-	-	-
Phylogenetic analyses	-	-	ITS (ITS1, 5.8S, ITS2)	-	-	-
Dinoflagellate occurrence examined in relation to	Other phytoplankton taxa, temperature, salinity, maximum sea ice cover, wintertime NAO, sampling location, time of sampling, eutrophication	Temperature, salinity, nutrients, chlorophyll *a*, sampling location, time of sampling	Temperature, salinity, sampling location, time of sampling	Temperature, salinity, nutrients, stratification, euphotic zone depth, sampling depth, time of sampling	-	-

[a] Sampling stations Längden, ENBP1 and ENBP2; for location see study IV.
[b] See text.
[c] See Rantajärvi & Leppänen (1994), Rantajärvi (2003), Algaline (2012), studies I–III.
[d] Sampled ship route as in studies I–III.
[e] Abundance estimations in ICES data according to ICES (1903a), in Algaline data according to HELCOM (2011b).
[f] According to HELCOM (2011b).
[g] According to Utermöhl (1958).
[h] Surface hauls (likely ~ 100 m in length, cf. Levander & Purasjoki 1947), and vertical hauls (10–0 m, 20–0 m).
[i] Water samples sedimented according to Utermöhl (1958).

northern sea areas from the northeastern Atlantic west of Ireland to the eastern Barents Sea (Kyle 1910) and was carried out by Finland, Sweden, Germany, Denmark, Russia, Norway, Holland, Belgium, England, Scotland, and Ireland. The Baltic Sea was investigated by the four first mentioned countries (in 1908 also Russia), and the data were published as plankton tables (ICES 1903a, 1904, 1905, 1907, 1908, 1909, 1912).

The resulting data are surprisingly extensive, but they are not homogeneous, as remarked already by Kyle (1910), Paulsen (1913) and Ostenfeld (1931); authors who produced early summaries of the investigation and its results. This is a consequence of international and national, as well as spatial and temporal, variation in the sampling strategies of the participating countries. To minimize the heterogeneity as far as possible and to ensure the best possible compatibility with the modern Algaline data (study I), we selected a subset of samples from the Finnish ICES data. Despite this, our historical dataset has exceptionally good coverage for the period: the 418 samples collected in the northern Baltic proper and the western Gulf of Finland in 1903–1911 represent seven springs (May), seven summers (July–August), and six autumns (October–November). For comparison, the modern Algaline monitoring data, collected in 1993–2005, consist of 755 samples representing 13 springs, 13 summers, and 11 autumns (study I).

4.1.2. Historical phytoplankton methodology and steps taken to ensure compatibility with modern data

Somewhat unfortunately (but perhaps not unexpectedly), details of the early 1900s sample collection, treatment and microscopy, including how large a fraction of the net sample was analysed and with which equipment and accuracy, were not published (cf. ICES 1903a, 1904, 1905, 1907, 1908, 1909, 1912, Kyle 1910). In 1902, a proposal for the plankton methodology was made by P.T. Cleve and C.H. Ostenfeld (ICES 1903b), and in 1903 instructions for participating countries were issued in an ICES special circular (No. 4, on 26 January 1903, no longer available; mentioned in ICES 1903b: XXIV–XXV); later, the recommendations were revised (ICES 1910). The degree to which the instructions were applied was not disclosed; we suspect that not very strictly, based on the (both international and national) heterogeneity of the data (study I).

Since the lack of detailed information prevented us from replicating the sampling procedures and, by performing parallel samplings, comparing the results obtained with historical and modern techniques, we used our own experience and published information in assessing the historical material (study I). Published information was available in the form of contemporary reviews and synopses of the ICES data (Kyle 1910, Ostenfeld 1906, 1910, 1913a, 1913b, 1916, 1931, Ostenfeld & Wesenberg-Lund 1909, Paulsen 1913) and of the methodology (e.g. Lohmann 1901, 1908), as well as additions and corrections to the plankton tables (ICES 1907: 193). We also inspected original notes and drawings by K.M. Levander, the main analyst of the Finnish ICES data, dating from the late 1800s to the early 1900s. In comparison to the high-tech equipment available today, the microscopes one hundred years ago were fairly simple. For example, phase-contrast optics, which greatly enhances the distinguishing of cellular details, was developed only in the 1950s (Ruzin 1999). However, as testified

by some stunningly detailed drawings from the late 1800s to the early 1900s (e.g. Levander 1894), the precision of both the microscopes and the analysts should not be underestimated.

The major difference between the historical ICES data and the modern Algaline data was that the former consisted of net sample data, the latter of discrete water sample data (Table 1, study I). The mesh size (mesh diagonal) of the utilized Müllergaze Nr. 20 nets was in the range 43–115.5 µm (Lohmann 1901 and references therein). However, Lohmann (1901) found that 1 cm^2 of this silk gauze fabric consisted of 0.86 cm^2 of thread and 0.14 cm^2 of "hole", and that the coarseness (3-dimensional structure) of the fabric weave promoted the entrapment of cells that were smaller than the mesh size. Moreover, the mesh size of plankton nets tended to become smaller with use (Lohmann 1901 and references therein), and also, particularly during high-biomass periods such as the seasons we studied (spring, summer, autumn; study I), the nominal mesh size, and therefore the catch-loss, decreased as the (larger) organisms clogged the nets progressively during the haul (cf. Lohmann 1901, 1908, Ostenfeld 1910, Paulsen 1913).

Many taxa occurring in the Baltic Sea are fairly small-sized compared with those of the same taxonomical affiliation that occur in full-salinity marine environments. Based on Lohmann's (1908) comparison of different methods, Wasmund et al. (2008) concluded that when Müllergaze Nr. 20 nets were used, e.g. *Dinophysis* species were not reliably *quantitatively* sampled. Paulsen (1913), although expressing some concern that smaller dinoflagellates were not reliably sampled in the ICES monitoring, considered the *semi-quantitative* records of *Dinophysis acuminata*, *D. norvegica* and *D. rotundata* to be fairly accurate and uniform.

The catching of organisms smaller than the nominal mesh size is particularly clearly demonstrated by the results of Hessle & Vallin (1934), who in their investigation of Baltic Sea plankton used a zooplankton net with a mesh size of ca 200 µm. Even with this equipment they caught specimens of *D. acuminata*, *D. norvegica*, *Thalassiosira baltica* and *Actinocyclus octonarius* (Hessle & Vallin 1934), all considerably smaller than 200 µm (Olenina et al. 2006).

The net hauls (both horizontal and vertical) were at least several metres in length (Table 1, study I), i.e. they covered a substantial volume of water. Therefore, both fairly small-sized and sparsely occurring species were probably as likely caught with the net sampling, as in the discrete water samples with a volume of merely 50 ml, which were analysed for the modern data. However, it is possible that both phytoplankton and zooplankton species compositions were analysed from the same (sub)sample in the historical data (see ICES 1903a, 1904, 1905, 1907, 1908, 1909, 1912). Thus there is a risk that the larger and therefore more prominent zooplankton species may have drawn attention from smaller-sized and/or more sparsely occurring phytoplankton species. Taking all this into account, we considered it best to eliminate small-sized taxa, and to be on the safe side, those that occurred very rarely (study I).

Perhaps the single most arduous part of study I was preparing the phytoplankton species data for analysis. The taxonomical nomenclature was updated, principally according to G. Hällfors (2004). We excluded:

(1) taxa too small to be reliably sampled with nets (largest cell dimension about ≤ 40 µm, including easily disintegrating small-celled colonies; information on cell sizes available e.g. in Olenina et al. 2006);

(2) taxa described in 1903 or later (cf. G. Hällfors 2004);

(3) taxonomically problematic taxa, consisting mainly of genus- or higher-level taxa which have been revised, or to which new taxa have been described, after 1903 (cf. G. Hällfors 2004);

(4) taxa not consistently recorded throughout the study period (applicable to the modern dataset only);

(5) taxa not belonging to phytoplankton (i.e. cysts, heliozoans, etc); and

(6) sporadic taxa occurring in < 5 % of samples in either dataset were excluded from both datasets to ensure that only reliably sampled taxa remained (study I).

Lastly, to better facilitate comparison of the datasets, or to take into account likely misidentifications and changes in species delimitations, some taxa were joined (study I). In total, 32 and 350 taxa were excluded from the historical and the modern datasets, respectively (not counting lower than species-level taxa, synonyms, or size classes). Most of the exclusions were due to small cell size or the description year being ≥ 1903. Depending on the analysis, we examined either all remaining 31 taxa (nine dinoflagellates, seven cyanophytes, 13 diatoms, one chrysophyte, and one chlorophyte; cf. study I), or a subset of these, i.e. the 20 taxa that occurred in both the historical and modern datasets (six dinoflagellates, three cyanophytes, nine diatoms, one chrysophyte, and one chlorophyte; study I, cf. Results and discussion Table 5).

4.1.3. Utilizing presence/absence data to compare taxon and group-wise occurrences

In both the historical ICES data and the modern Algaline data, phytoplankton abundances were estimated on a 5-level scale (study I). In order to minimize the effects of methodological differences when comparing the phytoplankton communities, we focused on the occurrence frequency of taxa; a robust measure since it utilizes simple presence/absence information. With abundance estimations an element of uncertainty comes into play (cf. Apstein 1904, HELCOM 2011b), particularly when applied to samples collected with different methods. We nevertheless consider the abundance data indicative of the relative amounts of the organisms in the samples and, while acknowledging its coarseness, utilized the semi-quantitative abundance data to the degree it was feasible, i.e. to identify dominant taxa.

Differences in the occurrence of the taxonomical groups included in the study, i.e. dinoflagellates, cyanophytes, diatoms, chrysophytes and chlorophytes, and the relative importance of these five groups in each season and both periods, were examined through a group-wise measure of presence/absence. This measure was obtained by summing up the mean occurrence frequencies of all taxa within each taxonomical group, and by calculating the percentage that each group's sum of mean occurrence frequencies constituted of the whole phytoplankton community's (all five groups') summed mean occurrence frequencies, for each season and year separately. Based on these annual seasonal figures, means representing each of the three seasons of the two periods were calculated. Thus both the number of taxa in a group and the occurrence frequency

Table 2. 5-level semi-quantitative abundance scale used for estimating taxon abundances (HELCOM 2011b). In this thesis, taxa occurring with either of the two highest abundance ranks (4–5) at least once were considered dominant.

Rank	Definition
1	very sparse, one or a few cells or units in the analysed area (i.e. in the sedimented sample)
2	sparse, slightly more cells or units in the analysed area
3	scattered, irrespective of the magnification several cells or units in many fields of view
4	abundant, irrespective of the magnification several cells or units in most fields of view
5	dominant, irrespective of the magnification many cells or units in every field of view

of these taxa influenced the group's mean occurrence frequency ratio (i.e. the group's relative importance), whereas the number of samples collected each year, and the number of years sampled, did not.

4.2. Semi-quantitative abundance scale (modern monitoring data, studies I–III)

In the Algaline data (studies I–III, this thesis A; Table 1), phytoplankton species abundances were estimated on a semi-quantitative 5-level abundance scale (HELCOM 2011b, Table 2). Provided that the same volume is always sedimented and examined, the samples are comparable (cf. Table 2); this was the case in studies I–III, and this thesis (this thesis A).

Although the more commonly used method is the quantitative phytoplankton analysis according to Utermöhl (1958; cf. Karlson et al. 2010), there are several benefits of using semi-quantitative abundance estimations. First, the semi-quantitative method is less time-consuming and thus facilitates the analysis of a large number of samples; in the 13-year period 1993–2005, a grand total of 2764 phytoplankton samples (study III) were analysed by a one-person workforce (S. Hällfors, substituted intermittently by M. Huttunen and the present author). Second,

the semi-quantitative method better takes into account even the smallest phytoplankton cells, the presence of which are often belittled when abundance is expressed in units of biomass. Third, community analysis with multivariate methods does not necessarily require quantitative data; unbiased qualitative data, in which the species abundances are in realistic proportions to each other (e.g. on scales of 0–5 or 0–10), are sufficient for the purpose (Sarvala 1984). Indeed, if the data consist of cell counts or biomasses, it is often necessary to use transformations that result in a roughly equivalent scale in any case (Sarvala 1984).

4.2.1. Recalculating semi-quantitative abundances when joining taxa

In studies I–II, some taxa were joined prior to data analysis. This was required to better facilitate comparison of the datasets, to take into account likely misidentifications and changes in species delimitations, and to dispose of excessive (taxonomically arbitrary) size classes. The rearrangement of taxa and size classes necessitated the recalculation of abundances, for which we developed a formula (study II, cf. H. Hällfors 2003). Due to the low number of abundance rank classes, the recalculation was conservative. When

two ranks were joined, the resulting rank equalled the higher of the two (e.g. 2+2→2, 2+3→3). When three ranks were fused, the resulting rank was the highest of the three (e.g. 1+3+4→4, 3+3+4→4, 3+4+4→4). Only the merging of three equal ranks resulted in a promotion of rank (e.g. 3+3+3→4; 5+5+5→5 being an obvious exception). In studies I–II a maximum of three taxa (or size classes) were joined in a sample. However, the same principle can be extended in joining more than three taxa, the prerequisite being that the joining is started from the lower order ranks, with three equal ranks resulting in promotion (e.g. 1+1+1+2+2+2+3→ 2+2+2+2+3→ 3+2+3 = 2+3+3→3).

4.3. Studying dinoflagellate occurrence and diversity using modern monitoring data (studies I–III)

4.3.1. Ships-of-opportunity: intensive surface layer sampling

In the early 1990s, the Finnish Institute of Marine Research began developing an automated flow-through monitoring system to be used on merchant ships as an alternative to using flow-through systems or traditional sampling on research vessels (cf. Rantajärvi & Leppänen 1994, Rantajärvi 2003). This aptly named ship-of-opportunity system, operating within the framework of Algaline phytoplankton monitoring, was designed to enable intensive long-term observation of fluctuations in the phytoplankton community and the onset of phytoplankton blooms (Rantajärvi et al. 1998a).

The representativeness of these ship-of-opportunity data obtained at a fixed depth with flow-through apparatus (studies I–III) was evaluated by Rantajärvi et al. (1998b) and Kononen et al. (1999). By comparing chlorophyll *a* levels of samples collected at a depth of 5 m, and integrated mean chlorophyll *a* values calculated from samples taken at 0–20 m, Rantajärvi and co-workers (1998b) concluded that overall, phytoplankton biomass is fairly evenly distributed in the euphotic surface layer in the Baltic Sea. Kononen and co-workers (1999) compared flow-through apparatus data with data acquired by a water sampler at the same depth (ca 5 m) and concluded that the values correlated. Hence it is safe to assume that the ship-of-opportunity method produces data that give a good picture of the phytoplankton community of the euphotic layer. However, while this type of data (studies I–III) gives a good representation of the "average" dinoflagellate community of the surface layer, uneven vertical distributions are not revealed. This motivated our investigation of the vertical distribution of dinoflagellates in surface waters (study IV).

4.3.2. Identifying dinoflagellates in preserved samples

The identification of dinoflagellates is based on a multitude of morphological features which vary with group or genus (cf. Hansen & Larsen 1992, Steidinger & Tangen 1996, Hoppenrath et al. 2009). Some of these characteristics can be distinguished using light microscopy, while others require more specialized methods such as epifluorescence or electron microscopy (cf. study III). In light microscopy, the identification of thecate dinoflagellates is largely based on thecal plate pattern, cell-surface ornamentation, size, shape, and proportions of the cell, and the structure and position of certain organelles. Athecate, i.e. naked species lacking thecal plates, as well as thecate species possessing very delicate armour, are determined using the latter characteristics.

When quantifying phytoplankton (studies I–IV), preservation (fixation) is necessary to immobilize swiftly moving flagellates. Also, when collecting large numbers of samples at a time (studies I–IV), preservation is needed to prevent the samples from changing before analysis. Although the impacts of different preservatives vary with phytoplankton group and species, all have some deleterious effects, distorting or masking features used for species identification (Throndsen 1978, G. Hällfors et al. 1979, Zaraus & Irigoien 2008). Athecate dinoflagellates should preferably not be preserved at all; they should be studied in the live state, since preservatives tend to deform the cells, even causing changes in cell size (Taylor 1978, Dodge 1982, 1984, Steidinger & Tangen 1996). The iodine-based acid Lugol's solution (Willén 1962) is the most suitable preservative for brackish-water phytoplankton (G. Hällfors et al. 1979) and recommended for usage in Baltic Sea phytoplankton monitoring (HELCOM 2011b); therefore it was used in this thesis (studies I–IV, this thesis). It too, however, has some downsides, the main one being that iodine stains the protoplasm, rendering the plate patterns and surface ornamentation of thecate taxa difficult to discern (Steidinger & Tangen 1996). For the same reason, the presence or absence of chloroplasts may be difficult to distinguish. In summary, not all dinoflagellates can be identified to species or even genus level in preserved samples.

Thus, when investigating dinoflagellates (or the whole phytoplankton community for that matter), it usually comes down to a choice between a detailed study of the species composition in a few samples using comparatively laborious and expensive specialized methods, or alternatively, studying the occurrence of fewer taxa using the less advanced methods, but gaining in spatial and temporal resolution. For the

purposes of this thesis, both options were utilized. Species identification in studies I–II, IV and this thesis (this thesis A–B) was based solely on light microscopic analysis of acid Lugol's preserved samples, while in study III advanced methods facilitating detailed species identification were applied in combination with methods utilized within routine phytoplankton monitoring.

5. RESULTS AND DISCUSSION

5.1. Dinoflagellate diversity in the northern Baltic Sea (studies II–III, this thesis)

Within the framework of this thesis, 47 dinoflagellate species, 28 genera, and four higher-level (combination) taxa were observed (Table 3). Of the species-level taxa, 15 have not been previously reported from the northern Baltic proper and/or the Gulf of Finland, i.e. *Prorocentrum cassubicum*, *P. micans, Gymnodinium stellatum, Torodinium robustum, Cladopyxis claytonii, C. setifera, Fragilidium subglobosum, Peridiniella danica* and *Polarella glacialis* (new to both sea areas; cf. G. Hällfors 2004, study II, this thesis Table 3), as well as *Cochlodinium* sp., *Kolkwitziella acuta, Kryptoperidinium foliaceum, Protoperidinium divergens*, *P. pallidum*, and *Pyrophacus horologium* (new to the northern Baltic proper; cf. G. Hällfors 2004, study II, this thesis Table 3).

We were also able to confirm the occurrence of five taxa, i.e. *Dinophysis acuta, Amphidinium sphenoides, Katodinium glaucum, Neoceratium tripos,* and *Gyrodinium fusiforme* (the latter tentatively; Table 3). Previous records of *D. acuta* from the northern Baltic Sea, particularly those dating to the early 1900s, are dubious, since

this species has frequently been confused with *D. norvegica* (G. Hällfors 2004, study I and references therein). The results of studies I–II (based in part on the same data) confirm the occurrence of *D. acuta* in both the northern Baltic proper and western Gulf of Finland presented by Edler et al. (1996). *Amphidinium sphenoides* has previously been reported from the northern Baltic Sea only by Suikkanen et al. (2007; cf. G. Hällfors 2004). From their paper, however, it is unclear whether they observed the species in the northern Baltic proper, or the Gulf of Finland, or both; our results (study II, this thesis) confirm that *A. sphenoides* occurs in both sea areas. *Katodinium glaucum* has been recorded from most parts of the Baltic Sea, but not the Gulf of Finland (G. Hällfors 2004). Moisander and co-workers (1997) reported it in their study, but again, it is not clear in which sea area they found it; study II and this thesis confirm the occurrence of *Katodinium glaucum* in the Gulf of Finland also. *Neoceratium tripos* mainly occurs in the southern Baltic Sea and previous records from the north were considered doubtful (G. Hällfors 2004); our results confirm the sporadic presence of this species in the Gulf of Finland (study II). Finally, *Gyrodinium fusiforme* was among the taxa listed by Suikkanen and co-workers (2007; sea area not specified). Investigating 18S rRNA gene diversity, Majaneva et al. (2012) found sequences matching this species in the Gulf of Finland. Our tentative identification of *Gyrodinium fusiforme* (as *G.* cf. *fusiforme*; this thesis Table 3) in combination with the above findings indicates that this species occurs in both the northern Baltic proper and the Gulf of Finland.

From the northern Baltic proper and the Gulf of Finland, G. Hällfors (2004) lists 30 dinoflagellate genera and 75 species (counting species denoted "sp." and "cf.", but not species, the records of which are indicated to be questionable). Although we found taxa not previously reported from the area, the number we observed was lower (28 genera and 47 species, same counting criteria applied; Table 3). There are two reasons for this discrepancy. First, the identification of many taxa requires either the observation of live cells or the utilization of special methods (see Materials and methods) not feasible within the framework of routine phytoplankton monitoring. Second, in the Gulf of Finland our study area covered only the western part of the Gulf and primarily its open waters, where the salinity is higher than in coastal waters, particularly in the eastern part. Of the species reported by G. Hällfors (2004) from the northern Baltic proper and the Gulf of Finland, 17 are freshwater dinoflagellates that do not tolerate the full salinity of the area; only one of these, *Kolkwitziella acuta*, occurred in our samples.

Some of the taxa (*Prorocentrum cassubicum, Amphidinium sphenoides, Torodinium robustum, Kryptoperidinium foliaceum, Protoperidinium divergens, P. pallidum, Fragilidium subglobosum, Pyrophacus horologium*, *Neoceratium tripos,* and the genera *Cochlodinium* and *Cladopyxis*), have a curious distribution, occurring in the south(west)ern and northern parts of the Baltic Sea but not in between (cf. G. Hällfors 2004, study II, this thesis Table 3). Such a disjunct distribution is rather uncommon for other than dinoflagellates restricted to low-salinity coastal waters (cf. G. Hällfors 2004). Since none of the above-listed taxa are particularly frequently occurring (Table 3), their distribution pattern may be due to a lack of observation or a lack of published information, rather than a lack of occurrence in the central areas of the Baltic Sea. However, investigating *Prorocentrum minimum*, a dinoflagellate that

Table 3. The 66 dinoflagellate taxa observed within the framework of this thesis. Data from study II are complemented with previously unpublished data (this thesis A–B, see Table 1), focusing particularly on taxa novel to the study area. Species previously not reported from the northern Baltic proper and/or the Gulf of Finland, as well as species the occurrence of which was confirmed within the framework of this thesis (cf. G. Hällfors and other references in study II), are indicated in boldface. Heterotrophic (non-chloroplast-bearing) taxa are indicated by asterix (following G. Hällfors 2004 or, if taxon not included in G. Hällfors 2004, following the original species descriptions). Occurrence is based on study II and indicated as follows: generalist =all monthly mean occurrence frequencies ≥ 50%, common =monthly mean occurrence frequency ≥ 20% in at least one month of the year; infrequent =monthly mean occurrence frequencies < 20%; sporadic =rarely encountered. Taxa occurring with either of the two highest abundance ranks (4–5) at least once were considered dominant. - =indicates data insufficient for determining occurrence and seasonality. With the exception of the description of *Heterocapsa arctica* subsp. *frigida* (study III), identification is based on acid Lugol's preserved samples using light microscopy (phase contrast and differential interference contrast). Nomenclature follows G. Hällfors (2004) unless otherwise indicated. [App. 1] refers to taxonomical, nomenclatural, and identification-related annotations given in Appendix 1.

Taxon	Area	Occurrence [a]	Main season	Reference
PROROCENTRALES				
Prorocentrum balticum (Lohmann) Loeblich III	NBP, WGF	common	summer–autumn	II
***Prorocentrum cassubicum* (Woloszyńska) Dodge** [b]	**NBP, WGF**	sporadic	-	II, this thesis A
***Prorocentrum micans* Ehrenberg** [App. 1]	**NBP, WGF**	sporadic	-	II, this thesis A
Prorocentrum minimum (Pavillard) Schiller [App. 1]	NBP, WGF	common, dominant	summer–autumn	II
Prorocentrum spp.	NBP, WGF	sporadic	-	II, this thesis A, B
DINOPHYSALES				
Dinophysis acuminata Claparède & Lachmann	NBP, WGF	generalist, dominant	whole growing season	II, IV
***Dinophysis acuta* Ehrenberg**	**NBP, WGF**	infrequent	summer–autumn	II, this thesis A
Dinophysis norvegica Claparède & Lachmann	NBP, WGF	common, dominant	summer–autumn	II, IV
*Dinophysis rotundata Claparède & Lachmann	NBP, WGF	common	summer–autumn	II
Dinophysis spp.	NBP, WGF	sporadic	-	II
GYMNODINIALES				
*Amphidinium crassum Lohmann	NBP, WGF	common, dominant	summer–autumn	II
*Amphidinium cf. *longum* Lohmann	NBP, WGF	-	-	this thesis B
***Amphidinium sphenoides* Wulff** [App. 1]	**NBP, WGF**	common, dominant	spring	II, this thesis A, B
Amphidinium spp. (autotrophic) [App. 1]	NBP, WGF	sporadic	-	II
*Amphidinium spp. (heterotrophic) [App. 1]	NBP, WGF	infrequent	whole growing season	II
***Cochlodinium* sp.**	**NBP**, WGF	infrequent	whole growing season	II, this thesis A

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Species	Region	Abundance	Season	Source
Gymnodinium fissum Levander	NBP, WGF	common	whole growing season	II
***Gymnodinium stellatum* Hulburt** [c]	**NBP, WGF**	-	-	this thesis A, B
**Gymnodinium vestificii* Schütt	NBP, WGF	common	whole growing season	II
Gymnodinium spp. (autotrophic) [d, App.1]	NBP, WGF	generalist, dominant	whole growing season	II
**Gymnodinium* spp. (heterotrophic) [d, App.1]	NBP, WGF	generalist, dominant	whole growing season	II
***Gyrodinium* cf. *fusiforme* Kofoid & Swezy**	**NBP, WGF**	-	-	this thesis B
Gyrodinium spirale (Bergh) Kofoid & Swezy [App.1]	NBP, WGF	common	whole growing season	II
Gyrodinium spp. (autotrophic) [App.1]	NBP, WGF	infrequent	whole growing season	II
**Gyrodinium* spp. (heterotrophic) [App.1]	NBP, WGF	infrequent	whole growing season	II
***Katodinium glaucum* (Lebour) Loeblich III**	**NBP, WGF**	common	whole growing season	II, this thesis A, B
***Torodinium robustum* Kofoid & Swezy**	**NBP, WGF**	-	-	this thesis B
PERIDINIALES				
**Diplopsalis* group [e]	WGF	sporadic	-	II
Durinskia baltica (Levander) Carty & E.R. Cox	NBP, WGF	sporadic	-	II, this thesis A, B
Glenodinium spp. (autotrophic) [f, App.1]	NBP, WGF	common, dominant	summer–autumn	II
**Glenodinium* spp. (heterotrophic) [App.1]	NBP, WGF	sporadic	-	II
Heterocapsa rotundata (Lohmann) Hansen	NBP, WGF	generalist, dominant	whole growing season	II
Heterocapsa triquetra (Ehrenberg) Stein	NBP, WGF	common, dominant	summer–autumn	II
Heterocapsa arctica Horiguchi subsp. *frigida* Rintala & G. Hällförs [g]	NBP, WGF	common	spring	II, III
***Kolkwitziella acuta* (Apstein) Elbrächter**	**NBP**, WGF	sporadic	-	II
***Kryptoperidinium foliaceum* (Stein) Lindemann**	**NBP**, WGF	-	-	this thesis A
**Oblea rotunda* (Lebour) Balech ex Sournia [App.1]	NBP, WGF	common	summer–autumn	II
**Oblea rotunda* complex [App.1]	NBP, WGF	-	-	this thesis A, B
Peridinium spp.	NBP, WGF	sporadic	-	II
**Preperidinium meunieri* (Pavillard) Elbrächter	NBP, WGF	infrequent	summer–autumn	II
**Protoperidinium achromaticum* (Levander) Balech	NBP	sporadic	-	II
**Protoperidinium bipes* (Paulsen) Balech	NBP, WGF	common, dominant	spring	II
**Protoperidinium brevipes* (Paulsen) Balech	NBP, WGF	common, dominant	early summer	II

Species				
Protoperidinium divergens (Ehrenberg) Balech	**NBP**	sporadic	-	II
Protoperidinium granii (Ostenfeld) Balech	NBP, WGF	common	spring	II
Protoperidinium pallidum (Ostenfeld) Balech	**NBP**	sporadic	-	II
Protoperidinium pellucidum Bergh	NBP, WGF	common	spring	II
Protoperidinium spp.	NBP, WGF	common	whole growing season	II
Scrippsiella/Biecheleria/Gymnodinium complex [App. 1]	NBP, WGF	common, dominant	spring	II
Scrippsiella trochoidea (Stein) Loeblich III [App. 1]	NBP, WGF	infrequent	summer–autumn	II
GONYAULACALES				
Alexandrium ostenfeldii (Paulsen) Balech & Tangen [h, App. 1]	NBP, WGF	infrequent	whole growing season	II, this thesis A
Amylax triacantha (E. Jørgensen) Sournia [App. 1]	NBP, WGF	common, dominant	early summer	II
Cladopyxis claytonii R.W. Holmes	**NBP, WGF**	-	-	this thesis A, B
Cladopyxis setifera Lohmann	**NBP, WGF**	infrequent	summer–autumn	II, this thesis A, B
Cladopyxis spp.	WGF	-	-	this thesis B
Fragilidium subglobosum (von Stosch) Loeblich III [i]	**NBP, WGF**	infrequent	whole growing season	II, this thesis A
Gonyaulax spinifera (Claparède & Lachmann) Diesing [App. 1]	NBP, WGF	sporadic	-	II
Gonyaulax verior Sournia	NBP, WGF	infrequent	summer–autumn	II
Gonyaulax spp.	NBP, WGF	sporadic	-	II, this thesis A, B
Neoceratium tripos (O.F. Müller) F. Gómez, D. Moreira & P. López-García [j, App. 1]	**WGF**	sporadic	-	II
Peridiniella catenata (Levander) Balech	NBP, WGF	common, dominant	spring	II
Peridiniella danica (Paulsen) Okolodkov & Dodge [k, App. 1]	**NBP, WGF**	-	-	this thesis A, B
Protoceratium reticulatum (Claparède & Lachmann) Bütschli	NBP, WGF	common, dominant	summer–autumn	II
Pyrophacus horologium Stein [App. 1]	**NBP**, WGF	common	summer–autumn	II, this thesis A, B
SUESSIALES				
Polarella glacialis Montresor, Procaccini & Stoecker [l, App. 1]	**NBP, WGF**	-	-	this thesis A
AFFILIATION UNKNOWN				
(*Thecate dinoflagellate spp. [App. 1]	NBP, WGF	sporadic	-	II

[a] None of the 10 taxa with insufficient data to determine occurrence and seasonality occurred with a semi-quantitative abundance rank > 3 (data not shown).

[b] As *Prorocentrum* cf. *cassubicum* in study II.

[c] According to Hulburt (1957).

[d] In study II, both autotrophic and heterotrophic *Gymnodinium* spp. were divided into size classes (see Fig. 3). The smallest size class (10–15 µm) was the most commonly and abundantly occurring in both cases. For occurrence and seasonality of the other size classes see study II.

[e] Sensu Hansen & Larsen (1992).

[f] In study II, autotrophic *Glenodinium* spp. was divided into size classes (see Fig. 3). The smaller size class (10–20 µm) was the most commonly and abundantly occurring. For occurrence and seasonality of the other size class see study II.

[g] According to study III.

[h] As *Alexandrium* sp. in study II.

[i] As *Fragilidium* sp. in study II.

[j] According to Gómez et al. (2010); as *Ceratium tripos* in G. Hällfors (2004) and study II.

[k] Sensu Okolodkov & Dodge (1995).

[l] According to Montresor et al. (1999).

occurs throughout the Baltic Sea with the exception of the Gulf of Bothnia (G. Hällfors 2004, Olenina et al. 2010), Pertola and co-workers (2005) found that it occurred at the highest cell densities in the southern and northern parts of its distribution area. In the Gulf of Finland (but not in the Mecklenburg Bight in the south), the occurrence of *P. minimum* was strongly associated with the levels of total nitrogen, most of it organic (Pertola et al. 2005). The results of Pertola et al. (2005) suggest that mixotrophy, previously demonstrated for this species (Stoecker et al. 1997; see also Granéli et al. 1985), may play an important role in the nutrition of *P. minimum* in the northern Baltic Sea. Taking this hypothesis one step further, it is also possible that the disjunct distributions of the species observed within this thesis, most of which belong in the marine flora (cf. Steidinger & Tangen 1996, Bérard-Therriault et al. 1999, Throndsen et al. 2003, Hoppenrath et al. 2009) as opposed to the freshwater flora, are explained by the elevated level of organic compounds in the northern Baltic Sea.

5.1.1. Description of a new taxon and its occurrence – Heterocapsa arctica *subsp.* frigida

In study III, we contributed to the knowledge of Baltic Sea dinoflagellate diversity by formally describing a new taxon, *Heterocapsa arctica* subsp. *frigida* (study III, Table 3). The discovery of new phytoplankton species is not uncommon in the intensively investigated Baltic Sea, and very recently, two other vernal dinoflagellates were described; *Biecheleria baltica* by Moestrup et al. (2009), and *Gymnodinium corollarium* by Sundström et al. (2009). What makes our description of *Heterocapsa arctica* subsp. *frigida* (study

III) exceptional is the taxonomical unit of *subspecies*. Of the almost 2 000 species listed by G. Hällfors (2004) for the Baltic Sea, only four species have (a total of eight) subspecies among the valid synonyms. In connection with the formal description of *H. arctica* subsp. *frigida* in 2010 (study III), the original *H. arctica* Horiguchi (Horiguchi 1997) automatically received the epithet subsp. *arctica*. The importance of the usage of the subspecies epithets bears emphasizing; the short version, *H. arctica*, refers to both subspecies collectively.

Quite often new species are described with little (if any) ecological information (cf. Herman & Sweeney 1976, Horiguchi 1997, Iwataki et al. 2003, Tamura et al. 2005). Another feature that makes study III notable is thus that in connection with the formal description of subsp. *frigida*, we were able to provide extensive information regarding its occurrence and distribution. This was possible because due to its distinctive cell shape one of the authors, S. Hällfors, recorded the presence of subsp. *frigida* since the start of the Algaline phytoplankton monitoring programme.

Subspecies *arctica* was originally described from the Canadian Arctic (Horiguchi 1997), and to our knowledge it has been reported only from Canadian waters (cf. Bérard-Therriault et al. 1999, Riedel et al. 2003, Różańska et al. 2008, 2009). The conspecificity of *H. arctica* subsp. *frigida* with subsp. *arctica* was demonstrated by their practically identical ITS rDNA sequences in combination with similarities in morphological characteristics important in distinguishing between *Heterocapsa* species (i.e. body scale structure, shape and position of the nucleus, and ultrastructure and position of the pyrenoid; Hansen 1995, Iwataki 2008 and references therein) (study III). Despite the aforementioned similarities in genotype

and fine structure, the two dinoflagellates can easily be distinguished by their general morphology; *H. arctica* subsp. *frigida* is short and rounded compared with the considerably larger and more elongated subsp. *arctica* (study III).

Intraspecific differences in the cell size of some dinoflagellates have been attributed to differences in salinity (e.g. Leegaard 1920, Solum 1962, Pliński & Jóźwiak 1986). Since subsp. *frigida* occurs in the low-salinity Baltic Sea (studies II–III), and subsp. *arctica* in a full-salinity marine environment, the potential effect of salinity on cell size was investigated. Our results showed that although its cell size was slightly reduced when subcultured at a salinity of 6 (PSU) for a year, subsp. *arctica* did not "turn into" subsp. *frigida.* Despite a slight overlap in cell lengths, subsp. *arctica* remained significantly longer, wider, and thicker than subsp. *frigida*; thus the differences in morphology were salinity-independent (study III). According to the widely accepted definition of the taxonomical unit of subspecies by Du Rietz (1930: 354), a subspecies is a more or less distinct geographical variant of a species. Thus, based on the differences in general morphology and geographical distributions, the Baltic Sea *H. arctica* warranted the status of a new subspecies, subsp. *frigida* (study III).

While organisms with identical or almost identical ITS rDNA sequences are commonly considered to belong to the same species (Montresor et al. 2003a, study III), this is not necessarily always the case regarding dinoflagellates. An interesting case of identical genotypes associated with differing phenotypes, to consider in connection with *H. arctica*, is that of *Scrippsiella hangoei* and *Peridinium aciculiferum* (Gottschling et al. 2005, Logares et al. 2007). The former occurs in the brackish Baltic Sea [it is a member of the *Scrippsiella/Biecheleria/*

Gymnodinium complex sensu Sundström et al. (2010); cf. Table 3, study II], while the latter occurs in freshwater lakes in the Baltic Sea region (Logares et al. 2007). Based on their phenotypic differences and habitat segregation, it is not immediately apparent that they are very closely related; consequently despite their genotypical similarity, Logares and co-workers (2007) regarded them as separate species. Their speciation was explained by exposure of the ancestral populations to different selective pressures in their environments (Logares et al. 2007). It is likely that a similar recent diversification occurred in *H. arctica*, possibly after the last glaciations c. 10 000 years ago, as suggested by Logares et al. (2007) for *S. hangoei* and *P. aciculiferum* (study III). The history of the Baltic Sea basin before and during the last deglaciation is not well known, and contrasting theories have been put forward (Winterhalter et al. 1981 and references therein). However, the presence of Arctic marine diatoms in the Baltic Sea has been explained by an assumed connection with the Arctic Sea (Leegard 1920, Hasle & Syvertsen 1990); this connection, and its later closure, would help explain the arrival of *H. arctica* and its subsequent diversification into subsp. *frigida* (study III).

In protists, the delimitation of the different taxonomical levels is not always clear; this concerns variation both in morphological and molecular features. Unfortunately, citing a focus on evolutionary processes, Logares et al. (2007) did not discuss the implications of their findings on the taxonomical nomenclature of *S. hangoei* and *P. aciculiferum*; nor did they speculate on the possibility of considering them subspecies instead of different species (study III). While acknowledging the findings of Logares et al. (2007), we considered a more conservative

view, i.e. conspecifity but differing on the subspecies level, well-justified in the case of *H. arctica* (study III).

Heterocapsa arctica subsp. *frigida* is an evident cold-water dinoflagellate and a regular member of the spring bloom community (Rintala et al. 2009, studies II–III). Subspecies *frigida* usually occurs in low abundances (semi-quantitative abundance ranks 1–3; studies II–III), but it has been observed as bloom-forming under the ice in the coastal western Gulf of Finland (Niemi & Åström 1987, as *Heterocapsa* sp.; S. Hällfors & G. Hällfors personal communication). This bloom, with a peak abundance of 822 000 cells L^{-1}, occurred under the ice in mid-March (Niemi & Åström 1987). In early May 2012, abundances of 30 100–49 200 cells L^{-1} were recorded in the coastal Gulf of Finland, off Helsinki (author's unpublished observations from phytoplankton samples taken by the City of Helsinki Environment Centre for the mandatory monitoring of treated sewage water impacts in the Helsinki sea area). Although *Heterocapsa arctica* subsp. *frigida* occurs most frequently and abundantly in the northern sea areas, it occurs throughout the Baltic proper, as well as in the Mecklenburg Bight in the southern Baltic Sea (study III, Table 4).

5.2. Dinoflagellates as part of the northern Baltic Sea phytoplankton communities (studies I–II)

In the western Gulf of Finland and the northern Baltic proper, dinoflagellates commonly make up 50–95 % of the total nano- and micro-sized phytoplankton biomass, particularly during spring but also in summer (Niemi 1975, Kononen & Niemi 1984, 1986, Heiskanen 1993, Hajdu et al. 2000, Höglander et al. 2004, Pellikka et

al. 2007, Jaanus et al. 2011). The relative importance of dinoflagellates in comparison to cyanophytes, diatoms, chrysophytes, and chlorophytes is evident also based on occurrence frequency ratios (study I, Fig. 1). It may be argued that dinoflagellates as a group benefited from the exclusion of small-sized taxa (≤ 40 μm; study I), including ubiquitous members of the phytoplankton community such as nanoflagellates of various taxonomical affinities. However, ≤ 40 μm sized flagellates also include many seasonally or even throughout the growing season commonly occurring dinoflagellates such as *Amphidinium crassum*, *H. arctica* subsp. *frigida, Heterocapsa rotundata, H. triquetra, Prorocentrum minimum, Protoceratium reticulatum, Protoperidinium bipes*, *Gymnodinium* spp. (10–15 μm), *Glenodinium* spp. (10–20 μm), and the *Scrippsiella/Biecheleria/Gymnodinium* complex (cf. study II), evening out the basis for comparison. While our results regarding the relative importance of the different higher taxonomical groups were, to facilitate the comparison of historical and modern data, by necessity based on a selection of taxa (cf. study I), these taxa can be considered defining of the phytoplankton community (study I). This conclusion finds support in Edler's (1979) investigation of phytoplankton succession in the Baltic proper. Of the 14 species that accounted for the greater part of the community (small-sized unidentified flagellates and monads omitted; Edler 1979), 12 were among the taxa which occur during both periods in study I. Our investigation of the relative importance of the higher taxonomical groups in study I should be taken for what it is, i.e. a *partial* comparison of the phytoplankton communities. Nevertheless, considered together, the results of studies I–II serve to accentuate the fact that dinoflagellates are
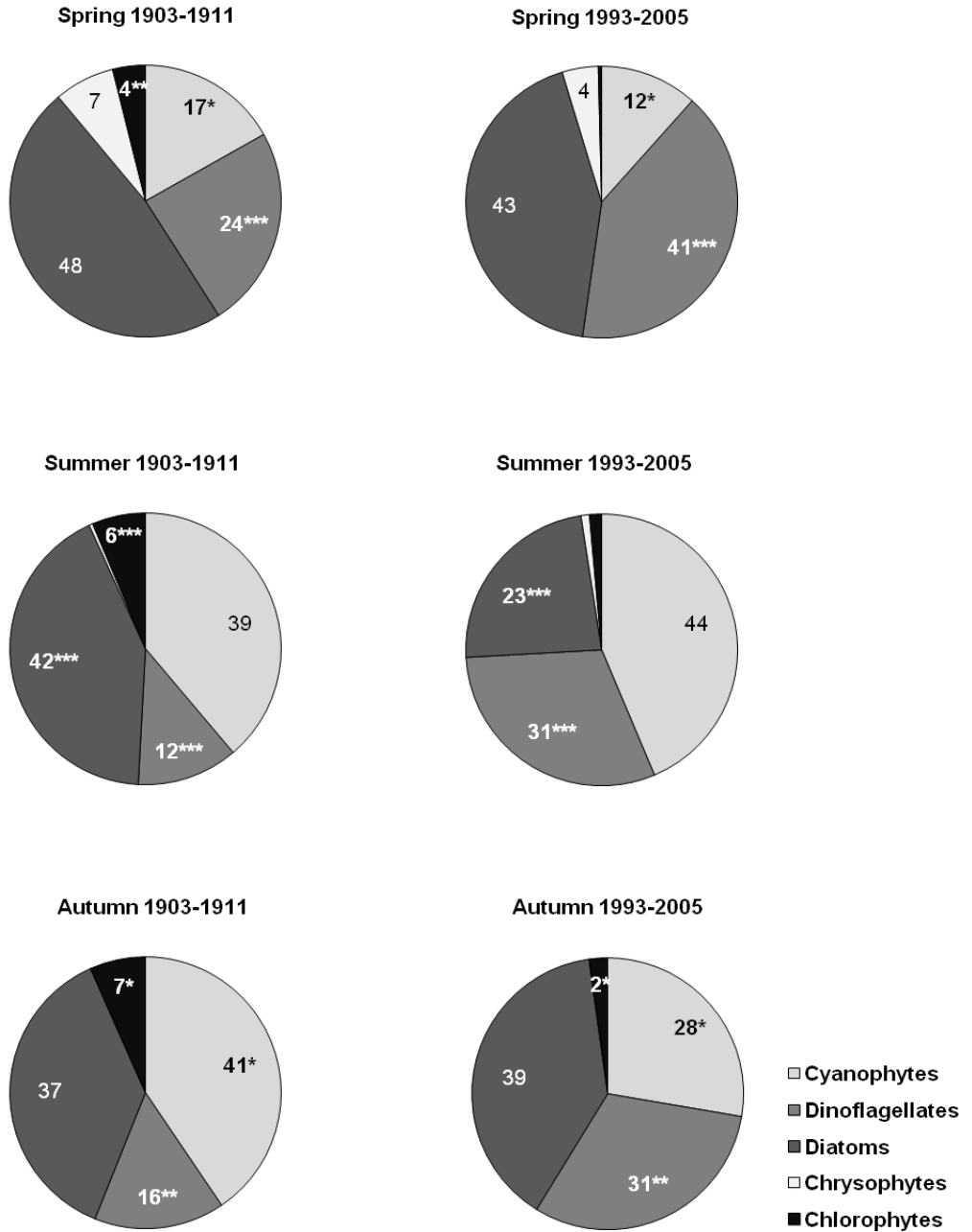
Fig. 1. Relative importance (mean occurrence frequency sum ratios) of the higher taxonomical groups in different seasons in 1903–1911 and 1993–2005, calculated based on the occurrence frequencies of 31 taxa (nine dinoflagellates, seven cyanophytes, 13 diatoms, one chrysophyte, and one chlorophyte). The ratios are rounded to whole numbers; for clarity, ratios < 2 % are not labelled. Asterisks indicate statistically significant differences between the two periods (Mann-Whitney U-test; *** < 0.001, 0.001 < ** < 0.01, 0.01 < * < 0.05). Note that for easy overview, the mean ratios for each period and season are presented; the non-parametric Mann-Whitney U-test does not, however, test for differences in datasets based on their means.

Table 4. Total number of phytoplankton samples, number of samples with *Heterocapsa arctica* subsp. *frigida*, and the occurrence frequency (percentage; unscaled to season or year) of subsp. *frigida* in the different areas of the Baltic Sea in 1993–2005. Sea areas delimited according to HELCOM (2006). Table modified from study III.

Baltic Sea area	Total n	*H. arctica* subsp. *frigida* n	%
Western Gulf of Finland	631	178	28.2
Northern Baltic proper	600	137	22.8
Eastern Baltic proper	327	41	12.5
Western Baltic proper	288	39	13.5
Southern Baltic proper	670	20	3.0
Mecklenburg Bight	248	3	1.2
Total all areas	**2764**	**418**	**15.1**

important members of the northern Baltic Sea phytoplankton community.

5.2.1. Dominant dinoflagellates

As judged by their semi-quantitative abundances, 16 of the 66 dinoflagellate taxa observed within the framework of this thesis dominated the phytoplankton community at one time or another (Table 3). Most of the dominant dinoflagellates were photosynthetic (Table 3). Even taking into account the different size classes of *Gymnodinium* spp. (treated collectively in Table 3, but see study II), only six heterotrophic taxa occurred as dominants, and all of them very rarely, i.e. in ≤ 1 % of the samples they occurred in (study II). This is in line with previous findings: despite their apparent importance as consumers (Bralewska & Witek 1995, Sherr & Sherr 2007), and constant presence (study II), heterotrophic dinoflagellates seldom form blooms (Larsen & Sournia 1991).

The dinoflagellates that regularly dominated the phytoplankton community were the well-known bloom-formers *Scrippsiella/Biecheleria/Gymnodinium* complex, *Peridiniella catenata*, and *Heterocapsa triquetra* (cf. Kremp 2000, Rantajärvi 1995, 1996, 1997, 1998, Lindholm & Nummelin 1999, Sundström et al. 2010). These were dominant in 53 %, 29 %, and 13 % of the samples they occurred in, respectively (study II). Perhaps a less expected result was that *Heterocapsa rotundata* was dominant in as many as 10 % of the samples it occurred in (study II), although also this species has previously been recorded among the dominants (Kononen et al. 1999, Rantajärvi 1997).

The toxin-producing *Dinophysis acuminata* (Lee et al. 1989; cf. Kuuppo et al. 2006) was dominant in 2 % of the samples it occurred in (study II). The peak of 14 300 cells L^{-1} we observed in August 2004 (study IV) is among the highest reported from the study area, surpassed only by an occurrence of about 25 000 cells L^{-1} reported by S. Hällfors & G. Hällfors (2007) off Helsinki. Of the other toxic or potentially toxic dinoflagellates observed, *Prorocentrum minimum* (toxic,

Grzebyk et al. 1997, Denardou-Queneherve et al. 1999; but see Kimor et al. 1985), *D. norvegica* (toxic, Lee et al. 1989; cf. Kuuppo et al. 2006), and *Protoceratium reticulatum* (toxic, Satake et al. 1997; cf. Uronen 2007) dominated in 5 %, 4 %, and < 1 % of the samples they occurred in, respectively, whereas *D. acuta* (toxic, Lee et al. 1989), *D. rotundata* (toxic, Lee et al. 1989; cf. Kuuppo et al. 2006), and *Alexandrium ostenfeldii* (toxic, Kremp et al. 2009, Hakanen et al. 2012) did not occur as dominants (study II).

Finally, although the properties and requirements of the individual species are likely obscured when several species are treated together (as in the taxa possessing the suffix "spp.", "group", or "complex"), the multi-species group *Gymnodinium* spp. (in the traditional sense of the genus, cf. Appendix 1) merits mentioning. Several of the most frequently encountered taxa were members of this genus, and many occurred as dominants (cf. study II and Figs. 2–3; the different size classes are considered collectively in Table 3). The occurrence and ecology of *Gymnodinium* spp. and other athecate dinoflagellates of the order Gymnodiniales are largely unknown, since only a few characteristic taxa can be identified to species level with the methods employed in routine monitoring work. Our results serve to demonstrate that athecate gymnodinioid dinoflagellates of the so called *Gymnodinium*-type are prominent members of the northern Baltic Sea dinoflagellate community, occurring as they do year-round and at times as dominants. They constitute both photosynthetic and heterotrophic species in both the nano- and microplankton size classes, thus covering a multitude of functional groups in the ecosystem. Furthermore, *Gymnodinium*-like dinoflagellates include toxin-producing members of, e.g. the genera *Karenia* and

Karlodinium, some of which elsewhere have caused extensive fish kills, and which may also be harmful to humans through their neurotoxic shellfish poisoning (NSP) toxins (e.g. Taylor et al. 2003).

5.2.2. Geographical distribution

The vast majority, i.e. 60 of the 66 dinoflagellate taxa observed within the framework of this thesis, occurred in both the northern Baltic proper and the western Gulf of Finland (Table 3; the remaining six taxa were all very rarely encountered). This result was anticipated; due to the similar prevailing environmental conditions and the lack of a natural border between the two sea areas, we did not expect to see marked geographical differences in the dinoflagellate species compositions within the study area.

Examining the northern Baltic proper and the Gulf of Finland separately, Suikkanen et al. (2007) found some differences in the long-term trends of the summertime phytoplankton communities of the two sea areas. However, investigating these areas together, we found that sampling location was not of importance in explaining variation in the phytoplankton communities [as indicated by latitude and longitude, based on non-metric multi-dimensional scaling analysis (nMDS), study I, Fig. 4], or in the dinoflagellate species composition [as indicated by longitude, based on canonical correspondence analysis (CCA), study II, Fig. 2]. These results are supported by a permutational multivariate analysis of variance using distance matrices performed in study I, in which the samples were divided into groups according to sampling location (open northern Baltic proper, open western Gulf of Finland, and coastal samples). The analysis revealed that location had little
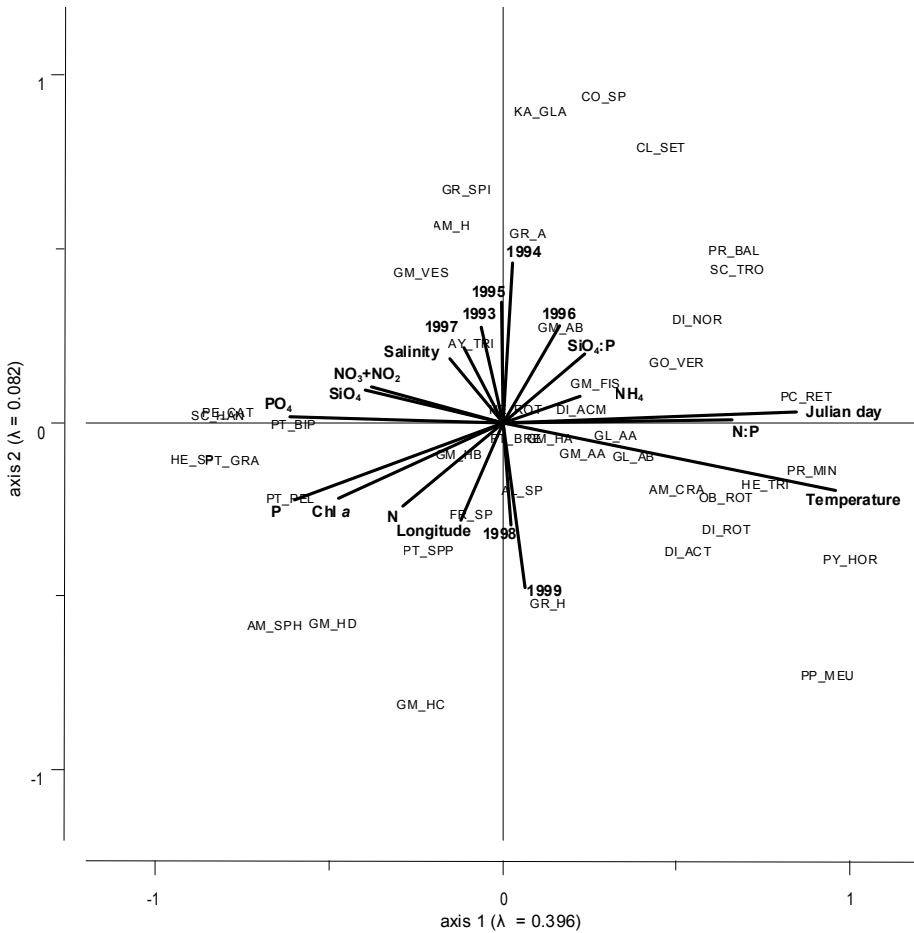
Fig. 2. CCA diagram showing the relationship between 44 dinoflagellate taxa and explanatory variables in 1993–2000. Taxa that have similar occurrences are situated close to each other. The relative lengths and directions of the arrows are of interest; important explanatory variables tend to be represented by longer arrows than less weighty variables. Arrows pointing in the same or in the opposite directions are correlated positively and negatively, respectively; orthogonal arrows are uncorrelated (e.g. ter Braak 1986, 1995, ter Braak & Verdonschot 1995). Taxon abbreviations are given in Fig. 3. The taxa situated on top of each other are, from left to right, HE_SP and PT_GRA (just below axis 1), SC_HAN and PE_CAT (immediately above axis 1), and PT_BRE and GM_HA (just below axis 1 near centre of diagram), respectively. The importance of the axes in explaining variation in the species data are indicated by their eigenvalues (λ); the greater the value, the more important the axis. Figure from study II; for numerical information on CCA results see study II.

explanatory power regarding variation in the phytoplankton community (study I). Also in a preliminary CCA performed on the data of study II, the samples were divided into groups according to sampling location [the northern Baltic proper, the western Gulf of Finland, as well as the dynamic frontal zone at the entrance to the Gulf of Finland (cf. Kononen et al. 1996), and the coastal area off Helsinki; cf. H. Hällfors (2003)]. Since this geographical grouping explained only a minor fraction of the variation in the dinoflagellate community, it was excluded from the final analysis presented in study II. In summary, based on our results (studies I–II), the dinoflagellate communities of the northern Baltic proper and the western Gulf of Finland did not differ markedly.

5.3. Annual succession of dinoflagellates in the northern Baltic Sea (studies I–II)

The phytoplankton succession in the northern Baltic Sea is very seasonal in character (e.g. Edler 1979, G. Hällfors et al. 1981). This was reflected in the results of studies I–II, in which seasonality was the foremost feature that grouped taxa in the multivariate community analyses (nMDS in study I, along the first axis in Fig. 4; CCA in study II, along the first axis in Fig. 2). In study I, where the months May, July–August, and October–November were investigated during the two periods 1903–1911 and 1993–2005, the annual succession was not as extensively covered as in study II, which comprised data from February to November in 1993–2000. Hence below the focus will be on the results of study II.

The environmental parameters most important in describing the dinoflagellate species composition were temperature and Julian day (increasing along the first CCA axis; Fig. 2), as well as nutrients and phytoplankton biomass (decreasing along the first CCA axis; Fig. 2) (study II). Thus the first axis reflected the annual succession from dinoflagellates occurring in a high-biomass spring bloom phytoplankton community which thrives in cold, inorganic nutrient-rich waters, to dinoflagellates occurring later in the year in warm, inorganic nutrient-poor waters with a lower phytoplankton biomass. The dinoflagellates situated in the centre of the diagram comprised taxa which have a preference for the average values of the variables, as well as taxa apparently indifferent to variation along the examined environmental gradients (cf. ter Braak 1986, Bakker et al. 1990) (study II).

44 dinoflagellates were included in the community analysis (study II, Fig. 3). Based on the CCA (Figs. 2–3), and their monthly occurrence frequencies (cf. study II), the dinoflagellates formed five groups according to their seasonality: vernal, early summer, summer and autumn, throughout the growing season occurring, and generalist taxa (Fig. 3, Table 3). A sixth group was formed by 17 sporadically occurring dinoflagellates, excluded from the multivariate analysis due to their rare occurrences (study II, Table 3).

The seven spring bloom dinoflagellates (Fig. 3, Table 3) occurred most frequently and abundantly in (March–) April–May (–June). They occurred in temperatures up to 17° C, but were dominant only in temperatures < 8.5° C (study II). The smallest seasonal grouping was made up of three early summer taxa. Although these occurred in a wide range of temperatures, they displayed a distinct occurrence frequency peak in May or June (study II). Therefore their position along the first CCA axis (Fig. 3) is best explained by a preference for intermediate values, rather than an indifference to water temperature.
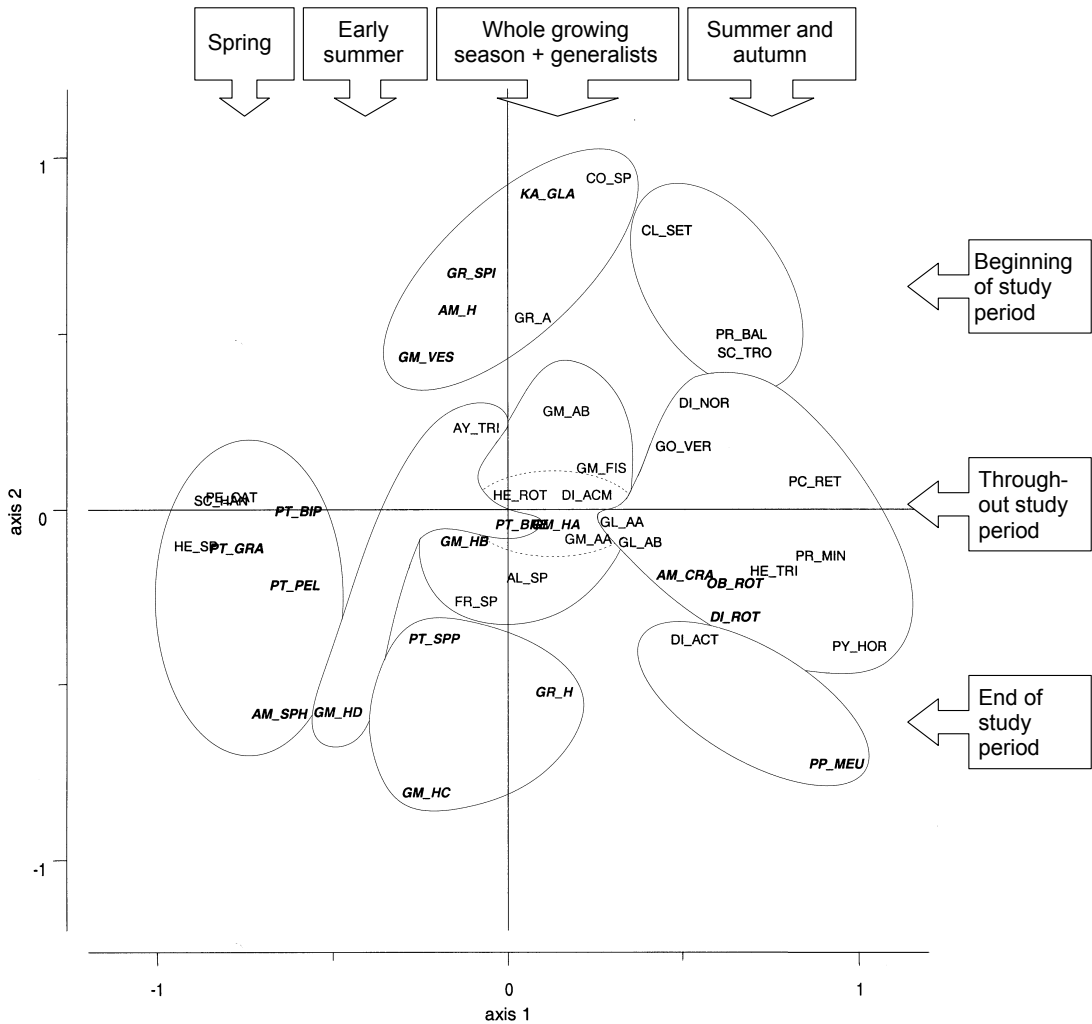
Fig. 3. CCA diagram showing the dinoflagellate seasonal groups and subgroups in 1993–2000. From left to right: vernal taxa, early summer taxa (bifurcate group), taxa occurring throughout the growing season, including the generalists (inside dotted line), and summer and autumn taxa. The taxa occurring throughout the growing season and the summer and autumn taxa formed three subgroups each, from top to bottom: taxa that occurred mainly at the beginning of the study period, taxa that occurred throughout the study period, and taxa that occurred mainly at the end of the study period. Heterotrophs are in boldface italics. The taxa situated on top of each other are, from left to right, HE_SP and PT_GRA (just below axis 1), SC_HAN and PE_CAT (immediately above axis 1), and PT_BRE and GM_HA (just below axis 1 near centre of diagram), respectively. The taxon abbreviations are ordered according to seasonal groups; within groups in the order from top to bottom according to the subgroups in the CCA diagram. Figure modified from study II.

VERNAL TAXA
    PE_CAT   *Peridiniella catenata*
    SC_HAN   *Scrippsiella/Biecheleria/Gymnodinium* complex
    PT_BIP   *Protoperidinium bipes*
    HE_SP   *Heterocapsa arctica* subsp*. frigida*
    PT_GRA   *Protoperidinium granii*
    PT_PEL   *Protoperidinium pellucidum*
    AM_SPH   *Amphidinium sphenoides*

EARLY SUMMER TAXA
    AY_TRI   *Amylax triacantha*
    PT_BRE   *Protoperidinium brevipes*
    GM_HD   *Gymnodinium* spp. d (heterotrophic > 55 μm)

TAXA OCCURRING THROUGHOUT THE GROWING SEASON
    CO_SP   *Cochlodinium* sp.
    KA_GLA   *Katodinium glaucum*
    GR_SPI   *Gyrodinium spirale*
    AM_H   *Amphidinium* spp. (heterotrophic)
    GR_A   *Gyrodinium* spp. (autotrophic)
    GM_VES   *Gymnodinium vestificii*
    GM_AB   *Gymnodinium* spp. b (autotrophic 15–65 μm)
    GM_FIS   *Gymnodinium fissum*
    GM_HB   *Gymnodinium* spp. b (heterotrophic 15–45 μm)
    AL_SP   *Alexandrium* sp.
    FR_SP   *Fragilidium* sp.
    PT_SPP   *Protoperidinium* spp.
    GR_H   *Gyrodinium* spp. (heterotrophic)
    GM_HC   *Gymnodinium* spp. c (heterotrophic 45–55 μm)

GENERALISTS
    HE_ROT   *Heterocapsa rotundata*
    DI_ACM   *Dinophysis acuminata*
    GM_HA   *Gymnodinium* spp. a (heterotrophic 10–15 μm)
    GM_AA   *Gymnodinium* spp. a (autotrophic 10–15μm)

SUMMER AND AUTUMN TAXA
    CL_SET   *Cladopyxis setifera*
    PR_BAL   *Prorocentrum balticum*
    SC_TRO   *Scrippsiella trochoidea*
    DI_NOR   *Dinophysis norvegica*
    GO_VER   *Gonyaulax verior*
    PC_RET   *Protoceratium reticulatum*
    GL_AA   *Glenodinium* spp. a (autotrophic 10–20 μm)
    GL_AB   *Glenodinium* spp. b (autotrophic 20–65 μm)
    PR_MIN   *Prorocentrum minimum*
    HE_TRI   *Heterocapsa triquetra*
    AM_CRA   *Amphidinium crassum*
    OB_ROT   *Oblea rotunda*
    DI_ROT   *Dinophysis rotundata*
    PY_HOR   *Pyrophacus horologium*
    DI_ACT   *Dinophysis acuta*
    PP_MEU   *Preperidinium meunieri*

The largest of the seasonal groupings, the summer and autumn dinoflagellates, constituted 16 dinoflagellates most of which are photosynthetic (Fig. 3, Table 3). The taxa attained their occurrence frequency peak during the warm-water period in (June–) July–August (–September) (study II). Most are recognized warm-water species (cf. G. Hällfors 2004), but all also occurred in temperatures < 10° C (study II). Fourteen dinoflagellate taxa were present throughout much of the year (Fig. 3, Table 3). Some of these occurred less frequently in early spring and/or late autumn, but all were present in April–October (study II). They usually occurred in low abundances and even the most common taxa did not form distinct seasonal occurrence frequency maxima; they tended however to occur slightly more frequently in spring–early summer and again in autumn. Thus their occurrence frequency dipped when that of the common summer and autumn taxa peaked (study II). The four generalist taxa were observed in February–November, with monthly mean occurrence frequencies always exceeding 50 % (study II, Fig. 3, Table 3). All generalists at one time or another occurred as dominants. While all seasonal groups occurred over wide temperature and salinity ranges, only the generalists were observed over the whole measured temperature (-1.2 – 21.7° C) and salinity (4.0–8.0) ranges (study II).

Overall, the arrangement of dinoflagellates into seasonal groups (study II) was consistent with published information. However, the verification of our results required an extensive literature review, demonstrating the demand for the compiled information presented in study II; in addition, some new findings transpired. *Protoperidinium pellucidum*, earlier a summer and warm-water species (cf. Kononen & Niemi 1984, G. Hällfors 2004, study I), is in fact currently a vernal species (studies I–II and references therein, Fig. 3). This may be related to the observed increase in summer and autumn water temperatures since the early 1900s (study I, cf. MacKenzie & Schiedek 2007); higher temperatures may be starting to restrict the occurrence of species such as this, which occurs in but is not strictly limited to cool waters (cf. G. Hällfors 2004). Another member of the same genus, *P. brevipes,* has been recorded from spring, summer and autumn assemblages (e.g. Niemi 1975, Niemi & Ray 1977, Suikkanen et al. 2007); previously no peak season was specified. Our results indicate that the main season of occurrence for this species is early summer (study II, Fig. 3). *Heterocapsa rotundata* is a generalist (study II, Fig. 3). Previously, it has been recorded in winter, spring and summer (e.g. Kuosa 1986, Autio et al. 1990, Rantajärvi 1995, 1996, 1997, 1998, Hajdu et al. 2007, Majaneva et al. 2012: Supplementary table 1), but no mention of its ubiquitous nature was found. It may have been overlooked due to its small size (cf. Olenina et al. 2006), or it may have been altogether lacking, in cases where nets were employed for sampling. Lastly, the seasonal distribution of taxa occurring throughout the growing season is worth noting; since no other publication with as high temporal coverage and taxonomical resolution of dinoflagellates in the northern Baltic Sea as study II exists, this information has previously not been presented (study II).

In summary, we found that on an annual scale, temperature in combination with season is to all intents and purposes a useful predictor of dinoflagellate species composition (study II, Figs. 2–3). This is in line with previous studies in which temperature was established as an important factor structuring the phytoplankton community in the northern Baltic Sea (e.g.

Gasiūnaitė et al. 2005). The degree to which phytoplankton species, dinoflagellates included, respond to temperature itself rather than related factors (cf. Kononen 1988) such as insolation, depth of the euphotic zone, and stratification, is however not clear.

5.3.1. Autotrophs and heterotrophs

Of the 66 dinoflagellate taxa observed within the framework of this thesis, 39 were autotrophic and 26 heterotrophic (for one taxon, unidentified thecate dinoflagellates, the mode of nutrition was not defined; Table 3). Of the 44 taxa included in the community analysis (CCA; study II, Figs. 2–3), 25 were autotrophic and 19 heterotrophic. Although these nutritionally differing dinoflagellates were not consistently separated into different seasonal groups (both autotrophic and heterotrophic taxa occur in all groups, Fig. 3), it is probable that the occurrences of the photosynthetic and the heterotrophic taxa are to some extent governed by different factors. Interestingly, the summer and autumn taxa as well as the generalists were predominantly photosynthetic; in the other three groups the ratio of photosynthetic and heterotrophic taxa was more even (Fig. 3). It is tempting to conclude that the predominance of chloroplast-bearing dinoflagellates in summer and (early) autumn is related to the high amount of available light. The causal relationships are however likely more complicated, since so many photosynthetic dinoflagellates are mixotrophs, i.e. also utilize dissolved and/or particulate organic matter for their nutrition (Gaines & Elbrächter 1987, Hansen 2011), and some apparently rely on kleptoplastids (Janson 2004, Minnhagen 2010) or temporary endosymbionts (Hansen 2011) as their photosynthetic machinery.

5.4. Changes in the occurrence of dinoflagellates: long-term shifts and interannual variation (studies I–II)

5.4.1. Community-level changes

We documented clear differences in the historical and modern phytoplankton communities, based on community analysis (along the second nMDS axis; Fig. 4), comparison of the relative importance of higher taxonomical groups (dinoflagellates, cyanophytes, diatoms, chrysophytes and chlorophytes; Fig. 1), as well as occurrence frequencies of individual taxa (in part presented in Fig. 5) (study I). Our result that the species compositions at the beginning and end of the 20th century differ is in agreement with findings from the Kattegat and Belt Sea area (Wasmund et al. 2008, Henriksen 2009, Skjevik & Edler 2011). Other than that, comparison of our results with the above studies is limited because the species compositions differ markedly, the southern flora being more oceanic in character due to the higher salinities (cf. Wasmund et al. 2008).

The relative importance of the higher taxonomical groups differed between 1903–1911 and 1993–2005 in all three seasons (study I, Fig. 1). The most obvious difference was the consistent and marked increase in the share of dinoflagellates at the expense of all other groups (in one or several seasons; Fig. 1). Perhaps most interesting is the decrease in the diatom to dinoflagellate ratio. Similar results have been obtained from different areas of the Baltic Sea, particularly for the spring bloom period, in several studies covering recent decades (Wasmund et al. 1998, Wasmund & Uhlig 2003, Pellikka et al. 2007, HELCOM 2009b, Klais et al. 2011). In contrast, in the Kiel Bight, the annual mean
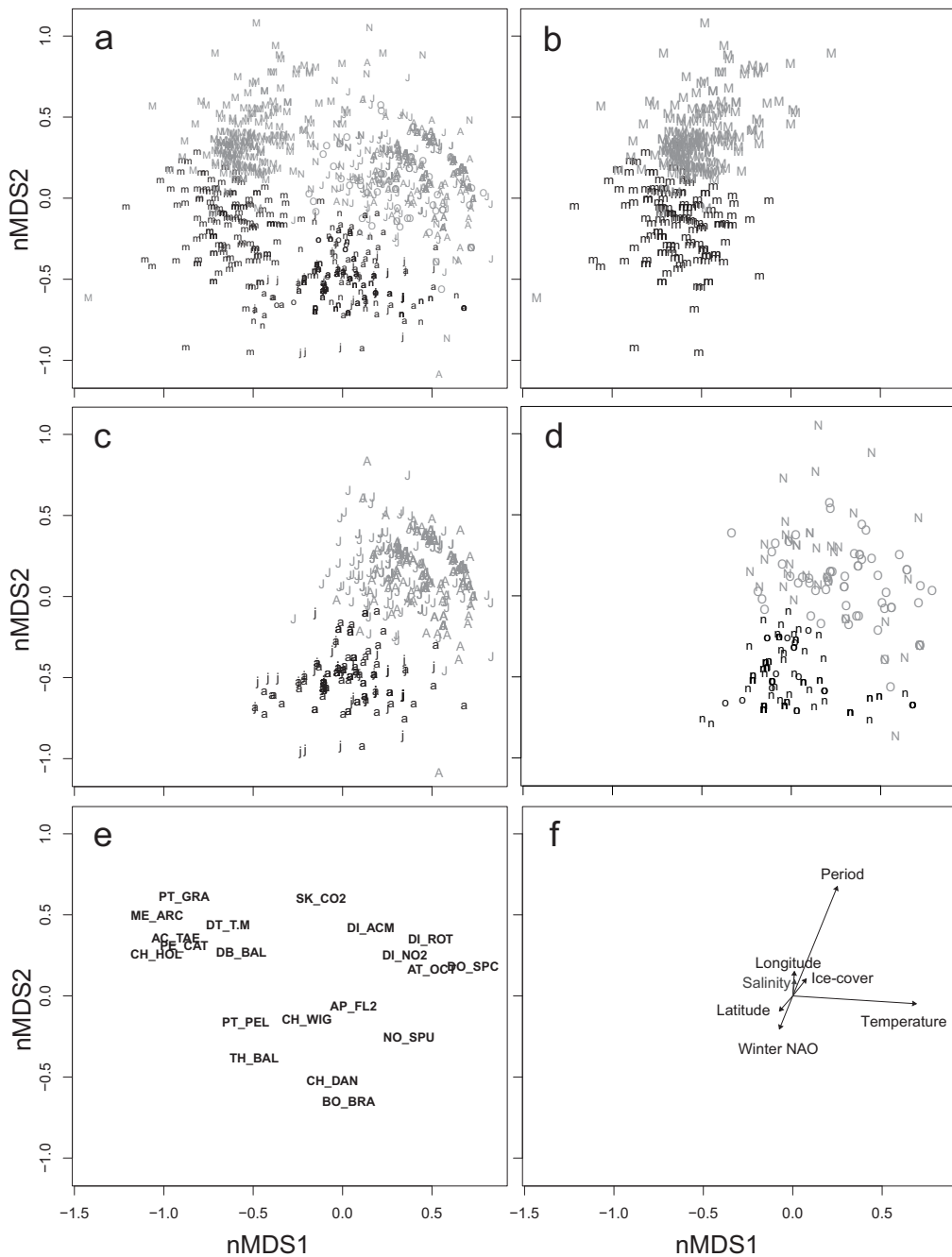
Fig. 4. nMDS ordination based on the presence/absence of the 20 phytoplankton taxa that occurred during both 1903–1911 and 1993–2005 (Table 5; the 11 taxa that occurred in only one of the two periods were excluded in order to explore differences in the communities beyond the obvious, study I). Similar samples, and taxa with similar occurrences, are positioned close to each other. The goodness-of-fit of the plot in presenting the original multi-dimensional dataset is indicated by the stress value; here stress = 0.189, indicating an acceptable fit of the nMDS ordination (e.g. Clarke & Warwick 1994). For clarity, the seasons (samples) and taxa are plotted separately: a) all samples, b) spring, c) summer, and d) autumn samples; the letters stand for May, July, August, October, and November samples, respectively, black lower-case used for historical data, grey capitals for modern data. e) taxa; for abbreviations see Table 5. f) independent environmental vectors fitted post-hoc (i.e. superimposed on the ordination); vector direction indicates direction of change, length indicates the strength of the correlation. Depicted vectors are significant (p < 0.001). Figure from study I.
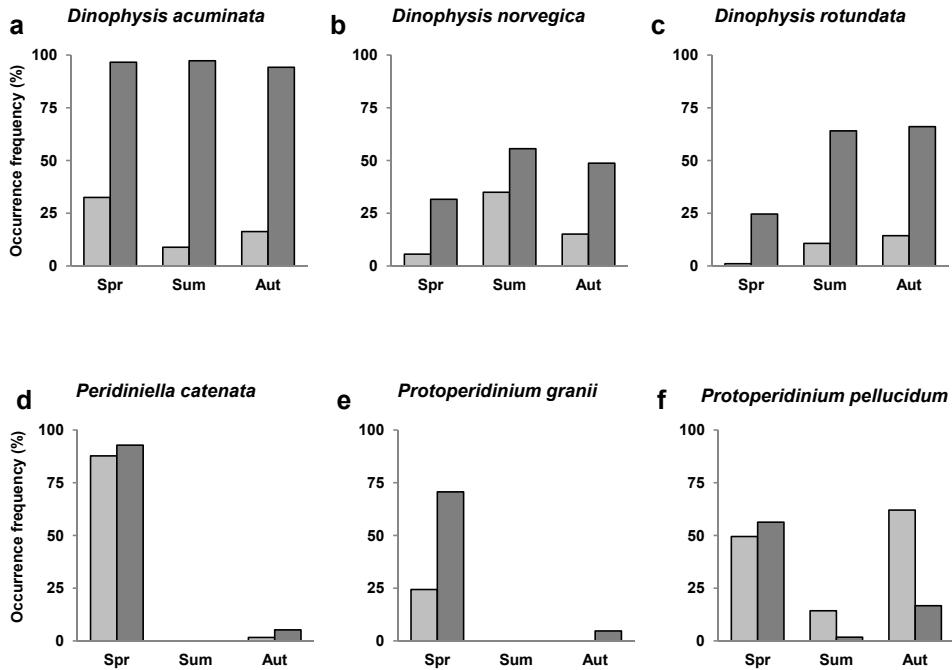
Fig. 5. Seasonal mean occurrence frequencies of the dinoflagellates that occurred in both 1903–1911 (left-hand columns) and 1993–2005 (right-hand columns), in spring (Spr), summer (Sum) and autumn (Aut). Figure modified from study I.

diatom to dinoflagellate biomass ratio did not alter during the course of the 20th century, based on data from the early and mid-1900s, as well as the early 2000s (Wasmund et al. 2008). While our results may indicate that conditions in our study area have generally shifted toward favouring dinoflagellates during the 20th century (study I), they are not conclusive; emerging evidence bespeaks a cyclic variation in the diatom to dinoflagellate ratio, with alternating dominance periods lasting about 10 years (Wasmund et al. 2011 and references therein). Since uninterrupted 100-year data series are not available, the oscillations or trends in the ratios of the

different groups could not be investigated within the framework of this thesis (study I). Hence we can conclude merely that the phytoplankton communities of the early and late 20th century differ.

Dinoflagellate occurrence varied not only in a centurial (study I) but also in a decadal time frame (study II). Even within the relatively short 8-year study period 1993–2000, a shift in dinoflagellate species composition took place, as revealed by the community analysis (along the second CCA axis; Figs. 2–3, study II). In the CCA diagram (Fig. 2), the arrows for the years 1993–1997 point in the opposite direction as the arrows

for 1998–1999; the year 2000 [being the reference dummy variable, cf. ter Braak (1995); study II] is located at the origin. Consistently, the taxa situated above the first CCA axis occurred mainly in the early years of the study, and those situated below the axis predominantly in the later years, while those situated close to the first axis occurred either without a clear interannual trend or fairly evenly throughout the study period (study II). When the eigenvalues of the first and second ordination axes differ greatly (as in this case; study II, Fig. 2), distances on the second axis are exaggerated (ter Braak & Verdonschot 1995). This means that the annual succession of dinoflagellates is of much greater importance than the interannual variation in explaining their occurrence, despite the apparent spread of taxa along the second CCA axis (Figs. 2–3). However, the variation in the interannual occurrences revealed by the CCA was confirmed by the annual mean occurrence frequencies of the individual taxa (study II, data not shown), and the shift could be discerned throughout the growing season (study II, Fig. 3), indicating that a factual change took place.

The shift in the dinoflagellate species composition during 1993–2000 was not as abrupt as might have been expected based on the positioning of arrows (and samples; see study II) in the CCA diagram (Fig. 2). It was a flowing transition characterized by an increase or decrease in occurrence, rather than by the appearance or complete disappearance of a large number of taxa at the turn of the years 1997–1998 (cf. Fig. 2). Indeed, the majority of the 44 dinoflagellates occurred without a trend, with nine taxa occurring predominantly at the beginning, and nine taxa mainly at the end, of the study period (Fig. 3; see also Table 3 in study II). An increase or decrease in occurrence was typical for the less commonly occurring taxa (study II). Those taxa that occurred throughout the study period appear to be established in the northern Baltic Sea, while the others are less well adapted and occur (or occur more frequently and abundantly) only when certain criteria are met. Specialized species with narrow ecological niches are more vulnerable to disruptions of their environmental requirements (Smayda 2002).

5.4.2. Changes in the occurrence of individual taxa

In study I, the historical and present-day occurrence of six dinoflagellate species (*Dinophysis acuminata, D. norvegica, D. rotundata, Peridiniella catenata, Protoperidinium granii* and *P. pellucidum*) was compared. Of these, all but one increased in occurrence frequency (*P. pellucidum*, Fig. 5), which is in line with the success of the group as a whole (study I, Fig. 1).

Worth noting is the pronounced increase in the occurrence of *Dinophysis acuminata, D. norvegica*, and *D. rotundata* in all seasons (study I, Fig. 5a–c). They are all potentially harmful due to their toxicity (Lee et al. 1989, Kuuppo et al. 2006). Their present-day occurrence seems to be stable; they did not display an increase or decrease in their occurrence in 1993–2000 (study II, Fig. 3). As discussed above, the fourth member of the genus, *D. acuta,* appears to be a fairly recent newcomer to the northern Baltic Sea; it may have expanded into the area as recently as the late 1980s–early 1990s (Edler et al. 1996). This species was one of the taxa that displayed an increased occurrence during 1993–2000 (study II, Fig. 3). Our finding that *D. acuta* became more common suggests that it has the potential to become established in the area; in the last year of the study (2000) it occurred in 22 % of samples (study II). In

contrast, *Prorocentrum minimum*, the other recent newcomer to the northern Baltic Sea, did not display a trend in its ocurrence (study II, Fig. 3). We found *P. minimum* in all years in 1993–2000, occurring in 9–45 % of samples (study II). We take this lack of trend as an indication of its ability to quickly establish itself in new areas (cf. Hajdu et al. 2000).

The occurrence of *Peridiniella catenata* did not markedly change from 1903–1911 to 1993–2005 (Fig. 5d, Table 5); the species was a frequent member of the spring bloom community already at the turn of the 20th century (Levander 1894, Paulsen 1913, study I). Indeed, until the early 1980s the spring bloom assemblage in the northern Baltic Sea was referred to as the "diatom–*Gonyaulax*" community (Välikangas 1926, Niemi 1973, 1975, Forsskåhl 1980); *Gonyaulax* indicating *G. catenata*, synonymous with *Peridiniella catenata* (G. Hällfors 2004). Members of the *Scrippsiella/Biecheleria/Gymnodinium* complex (cf. Appendix 1), today important components of the spring bloom community (e.g. study II), were not as prominent in the 1970s (G. Hällfors personal communication) and the 1980s–early 1990s (Kuosa et al. 1996, Wasmund et al. 1996) as they are now. In the 1990s and 2000s, their importance became evident (cf. Heiskanen 1993, Larsen et al. 1995, Kremp 2000, Jaanus et al. 2006). Dinoflagellates of the *Scrippsiella/Biecheleria/Gymnodinium* complex cell size ($< 40\ \mu$m; cf. Larsen et al. 1995, Kremp et al. 2005, Moestrup et al. 2009, Sundström et al. 2009) were unfortunately not representatively sampled with the nets used in the early 1900s (see Materials and methods). Needless to say, it would have been interesting to see how important this species complex was in the vernal community one hundred years ago.

The vernal *Protoperidinium granii* became more frequently occurring in 1993– 2005 as compared to 1903–1911; moreover it expanded to a new season, autumn (Fig. 5e). In contrast, the occurrence of the only dinoflagellate that regressed, *P. pellucidum*, dwindled in autumn to the extent that it today can be considered a vernal species (study I, Fig. 5f; see above; cf. study II).

Since the late 1990s, *Alexandrium ostenfeldii* has repeatedly formed blooms in coastal areas of the Baltic Sea (Hajdu et al. 2006, Kremp et al. 2009, Hakanen et al. 2012). In study II, covering the period 1993–2000, the species was however observed infrequently (Table 3) and did not display an increase in its occurrence (study II, Fig. 3). The explanation for this is likely twofold; most of the blooms have occurred since 2000, and moreover in coastal waters (Hajdu et al. 2006, Kremp et al. 2009, Hakanen et al. 2012), i.e. outside the scope of study II and this thesis.

5.4.3. Causes of change

None of the examined environmental descriptors, i.e. water temperature, salinity, winter conditions (the maximum extent of sea ice cover), and large-scale climate variability [wintertime North Atlantic Oscillation (NAO)], explained the centurial shift in the phytoplankton community composition (study I, Fig. 4). Also the shift in the present-day dinoflagellate community remained unexplained by the investigated environmental parameters, i.e. temperature, salinity, nutrients and nutrient ratios, and phytoplankton biomass (chlorophyll *a*) (study II, Fig. 2).

The undefined "period effect", which set the historical and modern phytoplankton communities apart during all three seasons in the community analysis (along the second nMDS axis, Fig. 4), was the second most important explanatory factor (after

Table 5. Relative contributions of the 20 phytoplankton taxa that occurred during both 1903–1911 and 1993–2005, to the differences between the periods according to the SIMPER analysis (no scaling). Seasons investigated both together and separately. Taxa that displayed a consistent increase or decrease in all three seasons, i.e. potential eutrophication indicators, are indicated in boldface; the direction of change is indicated by + (increased occurrence), - (decreased occurrence), or 0 (no change); n.a. = not available, i.e. taxon did not occur in the season in question. Selected annotations regarding the taxonomical nomenclature are given below; for more information see study I. The abbreviations used in the nMDS analysis (Fig. 4) are given. Table modified from study I.

	Contribution to total dissimilarity (%)				Abbreviation in nMDS
	all seasons	spring	summer	autumn	
Increased taxa					
Dinophysis acuminata	+ 10.1	+ 9.2	+ 14.4	+ 12.2	**DI_ACM**
Skeletonema costatum sensu lato [a]	+ 7.7	+ 9.4	+ 8.4	+ 9.3	**SK_CO2**
Dinophysis rotundata	+ 6.4	+ 2.6	+ 9.7	+ 8.6	**DI_ROT**
Dinophysis norvegica	+ 6.0	+ 4.3	+ 8.3	+ 6.8	**DI_NO2**
Anabaena/Dolichospermum **spp. (coiled)** [b]	+ 6.0	+ 0.1	+10.4	+ 2.6	**DO_SPC**
Actinocyclus octonarius	+ 5.5	+ 2.0	+ 7.2	+ 9.9	**AT_OCT**
Achnanthes taeniata	+ 4.2	+ 5.8	n.a.	+ 0.6	AC_TAE
Protoperidinium granii	+ 3.2	+ 8.1	n.a.	+ 0.7	PT_GRA
Melosira arctica	+ 1.8	+ 5.8	n.a.	n.a.	ME_ARC
Total contribution	**50.9**	**47.3**	**58.4**	**50.7**	
Decreased taxa					
Thalassiosira baltica	- 8.4	- 3.9	- 11.7	- 11.1	**TH_BAL**
Chaetoceros danicus	- 7.3	- 9.0	- 8.4	- 4.7	**CH_DAN**
Botryococcus braunii sensu lato [c]	- 5.0	- 4.1	- 6.1	- 7.7	**BO_BRA**
Total contribution	**20.7**	**17.0**	**26.2**	**23.5**	
Taxa with inconsistent change					
Chaetoceros wighamii	- 6.2	- 5.4	- 8.6	+ 7.8	CH_WIG
Protoperidinium pellucidum	- 5.5	+ 7.0	- 2.4	- 9.7	PR_PEL
Nodularia spumigena	- 5.2	- 5.5	+ 1.9	- 6.6	NO_SPU
Peridiniella catenata	- 5.0	- 1.8	n.a.	+ 1.1	PE_CAT
Dinobryon balticum	- 3.4	- 7.0	+ 1.6	0	DB_BAL
Chaetoceros holsaticus	- 1.4	- 4.6	n.a.	+ 0.1	CH_HOL
Diatoma tenuis + D. moniliformis [d]	- 1.0	- 2.8	+ 0.6	+ 0.2	DT_T.M
Aphanizomenon flos-aquae	+ 0.6	+ 1.5	+ 0.5	- 0.2	AP_FL2
Total contribution	**28.3**	**35.6**	**15.6**	**25.7**	

seasonality) also according to a permutational multivariate analysis of variance (study I). Analysing summertime phytoplankton species data from the last four decades, Olli et al. (2011) found that the community changed gradually with time, a change which in the northern Baltic Sea overrode changes in all measured environmental parameters. Finding no clear association with ambient nutrient concentrations or known spatial eutrophication gradients, they concluded that the change could not be attributed to eutrophication; rather, the phytoplankton community is inherently in a constant state of change (Olli et al. 2011). However, their data were from a period when the system was already heavily affected by anthropogenic eutrophication, the increase in nutrients and productivity having started already in the 1950s–1960s even in open-sea areas (Andrén et al. 2000, Struck et al. 2000, Poutanen & Nikkilä 2001). In light of the documented sensitivity of phytoplankton communities to different nutrient levels (e.g. Gasiūnaitė et al. 2005, Carstensen & Heiskanen 2007, Suikkanen et al. 2007,

Jurgensone et al. 2011), it seems unlikely that eutrophication would not have had any noticeable effects on the Baltic Sea phytoplankton community composition in our century-spanning investigation. Lacking historical nutrient and chlorophyll *a* data, our evidence is circumstantial; however in light of the developments in the Baltic Sea, we are inclined to interpret the centurial "period effect" as evidence of the direct and/or indirect influence of eutrophication (study I).

While eutrophication (cf. Hallegraeff 1993) and the increase in dissolved (cf. Granéli et al. 1985, 1999, Purina et al. 2004, Fagerberg et al. 2009) and particulate organic matter (prey; cf. Burkholder et al. 2008) may favour many dinoflagellates, we still lack definitive answers as to which conditions favour dinoflagellates over diatoms in the Baltic Sea. This concerns even the vernal bloom when the competition between the groups is most pronounced. The plausible explanations seem to be linked to a combination of environmental conditions and the intrinsic characteristics of the organisms

[a] The diatom until recently identified as *Skeletonema costatum* constitutes several species which cannot reliably be separated using light microscopy (see Kooistra et al. 2008 and references therein). Since this discovery, all strains which have been investigated from the Baltic Sea have been identified as *S. marinoi* Sarno & Zingone (Kooistra et al. 2008 and references therein, Wasmund et al. 2008), whereas investigating 18S rRNA gene diversity in the Baltic Sea, Majaneva et al. (2012) found *S. grevillei* Sarno & Zingone. We refer to these *S. costatum*-like species collectively as *S. costatum sensu lato* in accordance with e.g. Kooistra et al. (2008).

[b] Planktic (as opposed to benthic or soil-inhabiting) species of *Anabaena* were transferred to the genus *Dolichospermum* (Ralfs ex Bornet & Flahault) Wacklin, Hoffmann & Komárek by Wacklin et al. (2009), but some of the taxa present in our data (study I) were not included in their study.

[c] The original description of *Botryococcus braunii* Kützing is short and uninformative, consequently different morphotypes constituting several species have been ascribed to this taxon (Komárek & Marvan 1992). Hence we refer to these *B. braunii*-like species collectively as *B. braunii sensu lato*.

[d] *Diatoma tenuis* and *D. moniliformis* have several synonyms dating from the 1800s to the early 1900s, mainly as varieties of *D. tenue/tenuis* and *D. elongatum* (G. Hällfors 2004). Due to the early confusion in taxonomy, these two species are treated together.

themselves: life-cycle strategies involving plentiful cyst production which combined with motility facilitate effective recruitment of dinoflagellates (Kremp et al. 2008, Klais et al. 2011); the production of diatom-inhibiting allelopathic substances by dinoflagellates (Suikkanen et al. 2011); warmer climatic conditions and earlier stratification of the water column favouring dinoflagellate bloom formation (Wasmund et al 1998); and ambient nutrient status, particularly dissolved silicate limitation of growth and resting spore formation of diatoms (Jurgensone et al. 2011, Klais et al. 2011).

Regarding individual dinoflagellate taxa; as pointed out already by Kononen & Niemi (1984), most phytoplankton species, even dominant ones, show great year-to-year fluctuations which do not directly correlate with the observed variations in environmental factors. Due to complex interactions in the planktic community it is possible that what seem to be unimportant shifts in environmental parameters affect the populations (and individual taxa) in subtle ways, causing a continuous change, the reasons for which are not always immediately apparent (cf. Olli et al. 2011). An important aspect to consider when investigating long-term data is the taxonomical nomenclature. Changes in the nomenclature and taxonomical affiliation, if not properly taken into account, would show up as a shift in species composition; the change would either be abrupt or flowing, depending on the data (e.g. the data in studies I–II). Within the framework of the present thesis, the utmost care was taken to eliminate artefacts caused by changes in nomenclature; thus the shifts observed in studies I–II are (in light of the present taxonomical delimitations) real.

Summarizing, the community analyses of both studies I and II gave reasonable presentations of the variation explained by the variables included (based on numerical information of the nMDS analysis, the permutational multivariate analysis of variance, and the CCA; cf. studies I–II), as also demonstrated by the expected and realized strong structuring effect of seasons on the communities (studies I–II, see above). Nevertheless, a large share of the variation in the historical and modern phytoplankton communities (study I) and the present-day dinoflagellate assemblages (study II) was due to differences not attributable to any of the included environmental parameters or variables relating to sampling time or location, and was therefore left unexplained. These results are typical of ecological studies (e.g. ter Braak & Verdonschot 1995, cf. Suikkanen et al. 2007), since only a fraction of all environmental variables have ever been quantified. Linking differences or changes in communities to probable causes is difficult; this is an inherent problem of all phytoplankton community investigations, irrespective of the investigated time frame, because the planktic ecosystem is a highly dynamic system in which the physical, chemical and biological factors (such as temperature, salinity, stratification, availability of light and nutrients, and the presence of grazers, predators, pathogens and competition) display a pronounced patchiness on both spatial and temporal scales (e.g. Dybern & Hansen 1989). Hence the factors affecting the phytoplankton species composition at any point in time are numerous and their order of priority is difficult to determine – provided they have been measured in the first place (cf. Smayda 2004).

5.4.4. Potential eutrophication indicators

In the Baltic Sea, comparisons of historical and modern phytoplankton communities (or species occurrences) have usually been motivated by the need to assess changes with respect to eutrophication (cf. Finni et al. 2001a, 2001b, Johansson & Wallström 2001, Primakov & Nikolaenko 2001, Heiskanen et al. 2005, Wasmund et al. 2008, Henriksen 2009, Skjevik & Edler 2011). Our study (study I) is one of the only two investigations in which changes in the phytoplankton community have actually been quantified, the other being the study by Wasmund et al. (2008) on the phytoplankton communities in the Kiel Bight, in the coastal southwestern Baltic Sea.

A good eutrophication indicator species responds clearly and consistently even to minor changes in nutrient levels (Carstensen & Heiskanen 2007). While this may sound uncomplicated enough, more often than not the complex and dynamic relationship between phytoplankton and its abiotic and biotic environment makes distinguishing the influence of any particular pressure difficult (cf. Smayda 2004, studies I–II).

Above we concluded that eutrophication likely was the most important cause for differences in the historical and modern phytoplankton communities (study I). Taking a very simplistic approach, from this follows that the taxa which by their consistent increase or decrease contributed most to the differences in the two periods are the ones indicative of the change in trophic status. Such taxa were the dinoflagellates *Dinophysis acuminata, D. norvegica, D. rotundata*; the diatoms *Skeletonema costatum sensu lato, Actinocyclus octonarius*, *Thalassiosira baltica*, *Chaetoceros danicus*; the chlorophyte *Botryococcus braunii sensu lato*; and the cyanophyte *Anabaena/Dolichospermum*

spp. (coiled) (study I, Table 5). All seasons considered together, these nine taxa alone stood for 62 % of the dissimilarity between the historical and modern phytoplankton communities [according to a similarity percentages analysis (SIMPER); study I, cf. Table 5]. The cyanophyte Oscillatoriales spp. constitutes another potential indicator (cf. Jaanus et al. 2009); these cyanophytes were not recorded in the early 1900s but in the present-day data they occurred in all seasons (study I).

However, although *D. acuminata* (Autio et al. 1990, Hajdu 2002), as well as *S. costatum* (*sensu lato*) and Oscillatoriales spp. (Jaanus et al. 2009) may be favoured by high-nutrient conditions, the applicability of these and the other above-mentioned taxa as indicators is doubtful. This is because both *D. acuminata* and *D. norvegica* are mixotrophic and *D. rotundata* is heterotrophic and utilize particulate organic matter (e.g. Jacobson & Andersen 1994) and are thus not (solely) dependent on dissolved nutrients for growth, whereas *S. costatum sensu lato, Botryococcus braunii sensu lato, Anabaena/Dolichospermum* spp. (coiled), and Oscillatoriales spp. likely each constitute several species which do not necessarily respond equally to pressures. Regarding *T. baltica*, we could not exclude that its decline was not temperature-related (cf. *Protoperidinium pellucidum*, study I), whereas Carstensen & Heiskanen (2007) demonstrated that *A. octonarius* was not sufficiently prompt in its responses to changing nutrient levels to be useful as an indicator species. Therefore, the only promising potential eutrophication indicator species was *C. danicus*; on a 100-year scale an increased occurrence frequency of this diatom could be indicative of a more balanced, i.e. lower, nitrogen:phosphate:silicate ratio. However, although the results of the SIMPER

analysis (study I, Table 5) generally reflected the direction of change in seasonal mean occurrence frequencies of these taxa correctly, *C. danicus* was an exception; when taking into account the uneven temporal distribution of samples, this species did not decrease in autumn (study I). This discrepancy, which simply resulted from the high variability of the species' occurrence within periods and the use of unscaled data in the SIMPER analysis, nevertheless mars the applicability of *C. danicus* as a eutrophication indicator species (study I).

In summary, our endeavour to find occurrence-frequency-based eutrophication bioindicators met with difficulties, since none of the 10 candidates fulfilled the criteria of good indicator species; no valid eutrophication indicator species could be identified (study I).

5.5. Vertical distribution of dinoflagellates: a case study with *Dinophysis acuminata* and *D. norvegica* (study IV)

Dinophysis acuminata is a very common species in the northern Baltic Sea (studies I–II); it is present throughout the year (Niemi 1971), even in sea ice (Huttunen & Niemi 1986). It often occurs at densities from less than 100 to a few thousand cells L^{-1} (e.g. Hajdu 2002, Kuuppo et al. 2006, study IV), it is however not uncommon to find it as a dominant and/or in high abundances in the northern Baltic Sea (e.g. Niemi & Ray 1975, Kuosa et al. 1996, Wasmund et al. 1996, S. Hällfors & G. Hällfors 2007, Sjöqvist & Lindholm 2011, studies II, IV). In the present study area, *D. norvegica* is usually not as abundantly and frequently occurring as *D. acuminata* (studies II, IV), or as it is in the central Baltic proper (cf. Carpenter et

al. 1995, Meyer-Harms & Pollehne 1998). However, also this species occurs abundantly and/or as a dominant in the northern Baltic proper and the Gulf of Finland (Kuosa et al. 1996, Wasmund et al. 1996, Hajdu et al. 2007, study II). Both *D. acuminata* and *D. norvegica* have become more frequently occurring since the early 1900s and appear to thrive in the present-day eutrophied northern Baltic Sea (study I).

The general hypothesis that *Dinophysis* species favour a particular water depth due to the availability of dissolved nutrients and/or food organisms has neither been challenged nor supported by *in situ* observations (Maestrini 1998). This is still true more than a decade later, but it seems safe to assume that nutrition is a primary driver. The relationship between inorganic nutrient concentrations and the occurrence of *D. acuminata* and *D. norvegica* has repeatedly been considered (e.g. Subba Rao et al. 1993, Johansson et al. 1996, Godhe et al. 2002), but correlations have been difficult to establish. The utilization of dissolved organic matter is yet to be demonstrated for *D. acuminata* (however see Lunven et al. 2005, Velo-Suarez et al. 2008) and *D. norvegica*, but it has been shown for other dinoflagellates (Carlsson & Granéli 1998 and references therein). Moreover, several studies show that *D. acuminata* and *D. norvegica* ingest particulate organic matter (e.g. Jacobson & Andersen 1994, Carvalho et al. 2008). Current knowledge suggests that an important nutritional incentive may be the distribution of prey organisms that are suitable as chloroplast sources. The utilization of kleptochloroplasts has been suggested for *Dinophysis* species (e.g. Janson 2004, Minnhagen 2010), including *D. norvegica* (Minnhagen et al. 2008) and *D. acuminata* (Park et al. 2006), although studies on the latter species have also yielded

contrasting results (Garcia-Cuetos et al. 2010); the issue is thus as yet unresolved. To add to the mix, Sjöqvist & Lindholm (2011) recently presented evidence for the interdependence between *D. acuminata*, *Teleaulax* spp. (the possible source of *D. acuminata* chloroplasts, cf. Park et al. 2006), and *Mesodinium rubrum* (the food of *D. acuminata* and possible chloroplast vector, cf. Park et al. 2006) in natural communities in the Åland Archipleago, northern Baltic Sea.

Since *D. acuminata* has only recently been cultured successfully (Park et al. 2006), and *D. norvegica* not at all, observations of natural populations are still essential to further our understanding of their ecology. In the Baltic Sea, the vertical distribution of *Dinophysis* species has usually only been studied for short periods of time and/or at low vertical sampling resolution (Carpenter et al. 1995, Olli 1999, Gisselson et al. 2002, Setälä et al. 2005, Kuuppo et al. 2006, Hajdu et al. 2007). Furthermore, *D. acuminata* and *D. norvegica* have seldom been investigated simultaneously. Their regular presence and tendency to form subsurface maxima (e.g. Kuosa 1990, Carpenter et al. 1995, Setälä et al. 2005, Hajdu et al. 2007) qualified *D. acuminata* and *D. norvegica* as suitable study objects in our investigation of the vertical distribution patterns of dinoflagellates (study IV). *Dinophysis* research is known to be plagued by ambiguous and inconsistent results and few easy answers (e.g. Carvalho et al. 2008). In compliance with this tradition, our results agreed with some previous findings while questioning others (study IV).

In general, *D. acuminata* and *D. norvegica* formed population maxima either (1) in the mixed and usually illuminated surface waters above 10 m depth, or (2) below 10 m, in or out of the euphotic zone but near the thermocline, coinciding with a nutricline (study IV). Importantly, when *D.*

acuminata and *D. norvegica* co-occurred, their abundances peaked at different depths (Fig. 6a–c); this was observed even when both species formed maxima in the surface layer (Fig. 6d). This finding indicates a consistent niche separation of these two very closely related (Edvardsen et al. 2003) dinoflagellates.

Dinophysis acuminata was usually found in the illuminated and nutrient-poor mixed surface layer (Fig. 6a–f). Active growth of the mixed surface layer populations seemingly requires rapid recycling of nutrients, and/or nutrient retrieval migration to facilitate photosynthesis, and/or the utilization of mixotrophy (study IV). *Dinophysis acuminata* formed pronounced subsurface maxima only in the presence of light and a distinct nutricline (Fig. 6g–h), where the prevailing conditions appeared to facilitate photosynthetic growth, but did not exclude mixotrophy. When the spring bloom consumed nutrients from water layers far deeper than the euphotic layer, *D. acuminata* did not seek out the thermocline region (Fig. 6a–f). This dependency on light, suggested by our results (study IV), is supported by recent experiments by Kim et al. (2008) and Riisgaard & Hansen (2009) on cultured *D. acuminata*.

Dinophysis norvegica, on the other hand, was not as adverse to darkness and predominantly formed subsurface peaks, even below the euphotic zone (Fig. 6a–b, i). Compared with the thermocline peaks of *D. acuminata,* those of *D. norvegica* coincided with a rather modest increase in dissolved inorganic nitrogen (DIN) and/or dissolved inorganic phosphorus (DIP). An active growth of *D. norvegica* thermocline populations would seemingly require the utilization of either heterotrophy (Carpenter et al. 1995, Gisselsson et al. 2002) or, from the perspective of these populations, a "light
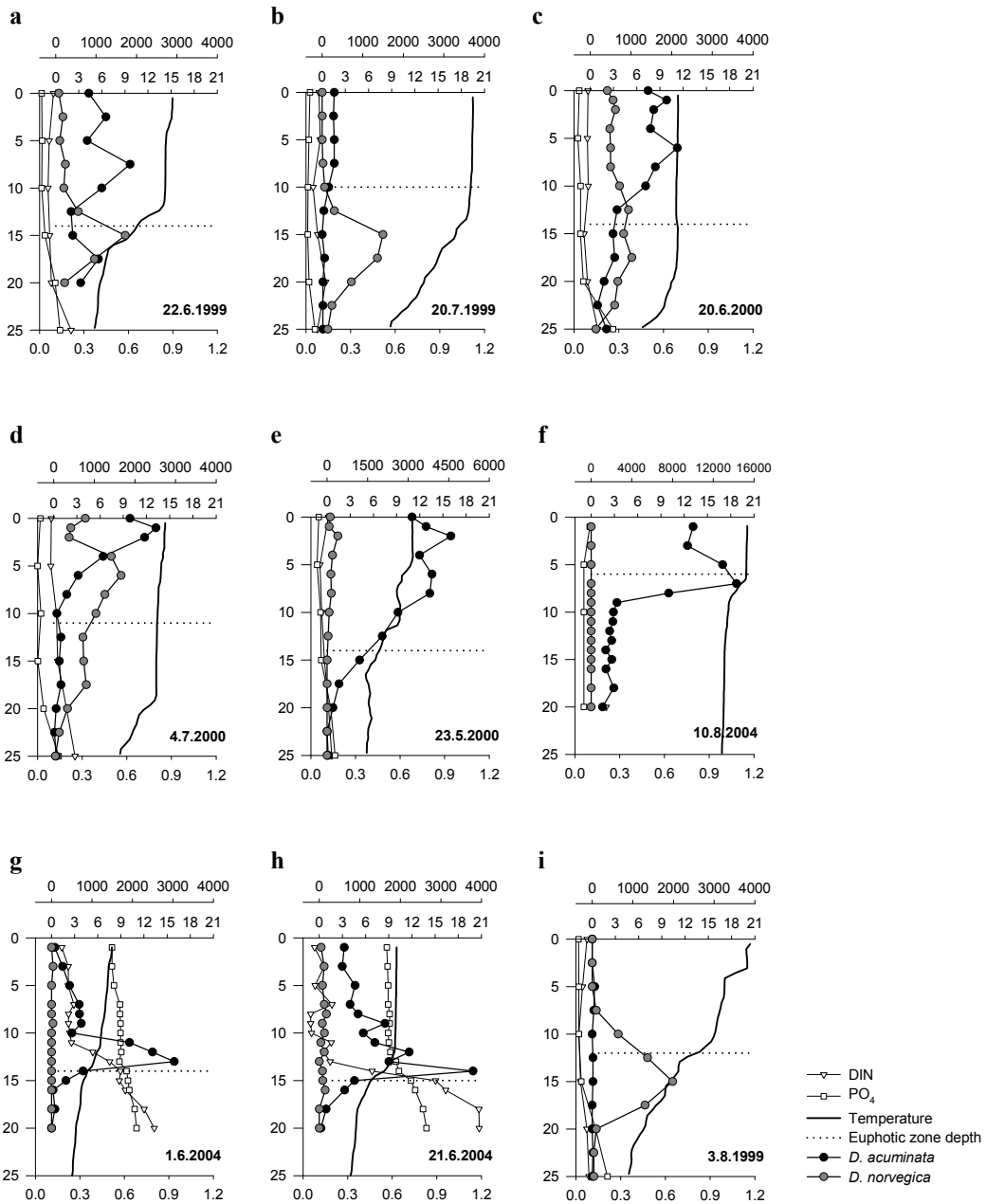
48

Fig. 6. Vertical profiles of *Dinophysis acuminata*, *D. norvegica*, and physicochemical parameters. Depth (m) on vertical axis. *Dinophysis* abundance on topmost horizontal scale (cells L⁻¹, note different scales), temperature (°C) on middle scale, and DIN and DIP (i.e. PO₄) concentrations (μmol L⁻¹) on lower scale. The nutrient curves should be considered indicative, since values below the detection limits (see study IV) were not excluded. The depth of the euphotic zone was calculated as twice the Secchi depth according to Niemi (1975), Højerslev (1978), and Aarup (2002). Vertical profiles with maximum cell densities < 250 cells L⁻¹ (study IV) were not considered when analysing the vertical distribution of the species, due to the low precision (large confidence limits) of the results when only a few cells were counted. Figure modified from study IV.

retrieval" migration, or a combination of both (study IV). However in a cool and deep mixed surface layer, generated by cool weather conditions and wind action during the *D. norvegica* peak season in summer, the species did not sustain clear subsurface maxima; instead it formed indistinct subsurface occurrences or remained in the mixed surface layer (Fig. 6c–d). This may indicate that the thermocline peaks are promoted by stratification at a fairly shallow depth (cf. Subba Rao et al. 1993, Gisselson et al. 2002), while mixing disrupts these subsurface populations (Gisselson et al. 2002). Alternatively, the lower surface water temperature and increased salinity induced by the mixing likely render the surface layer enviroment more suitable for this species (study IV and references therein), and it may in fact actively seek out the surface waters.

Active motility is an interesting feature to consider, facilitating as it does nutrient retrieval from deeper layers and thus the building up or sustaining of populations even in nutrient-poor surface waters (study IV). Both species have displayed impressingly high swimming speeds: for *D. norvegica*, Hajdu et al. (2002) observed a velocity of about 0.6 m h^{-1}; for *D. acuminata*, Lassus et al. (1990) estimated it as 0.7–1.1 m h^{-1} and Figueroa et al. (1998) as 1.5 m h^{-1}. Evidence for diel vertical migration in natural populations of *D. acuminata* has been presented by Villarino et al. (1995) and Figueroa et al. (1998), while *D. norvegica* has been found to display no (Carpenter et al. 1995) or only very limited (Hajdu et al. 2007) diel vertical migration. This observed lack of diel vertical migration may be accurate; possibly *D. norvegica* does not migrate with a daily rhythm, which considering its swimming capability would have to be explained by an absence of benefit from this behaviour. An apparently non-migratory population may, of course, also be in an inactive stage and therefore not migrating, or the apparent immobility may be an artefact caused by sampling strategies inadequate to detect (non-diel) migration patterns.

The possible existence of a non-diel migration pattern in *D. acuminata* and *D. norvegica* would explain why they reside by nutriclines at low light intensities, apparently displaying non-migratory behaviour. In some dinoflagellates, nutrient uptake rates are strongly dependent on light. MacIsaac (1978) found that DIN uptake rates in *Lingulodinium polyedrum* (as *Gonyaulax polyedra*) were similarly low during the night and at the bottom of the euphotic zone; high cell densities could not be attained unless DIN uptake was possible in illuminated conditions (MacIsaac 1978). If this is true for *D. acuminata* and *D. norvegica* also, they may have to remain at depth for longer than one night to accumulate enough nutrients for growth, and would then migrate to the near-surface layer to photosynthesize at non-diel intervals. Prolonged, non-diel vertical migration has been observed for other dinoflagellates (Kononen et al. 2003 and references therein), and also proposed for *D. acuminata* (Setälä et al. 2005).

Our finding that *D. norvegica* forms surface layer maxima (study IV), presents the possibility that it utilizes photoautotrophic nutrition to a greater extent than lately suggested (Carpenter et al. 1995, Gisselson et al. 2002, Carvalho et al. 2008). We ask, why would an organism have pigments (particularly if they are kleptochloroplasts, cf. Janson 2004, Carvalho et al. 2008, Minnhagen et al. 2008), which take up cellular space that could be used for food vacuoles, and which furthermore make the organism more easily spotted by predators, if not to use them at all? Unfortunately we have no data to validate or dispute the

utilization of photoautotrophy. It is however corroborated by the results of Mouritsen & Richardson (2003), who found that the vertical microscale distribution patterns of autotrophic and heterotrophic dinoflagellates differed significantly. While mixotrophs occurred in both groups, *D. acuminata* and *D. norvegica* grouped with the autotrophs (Mouritsen & Richardson 2003).

In summary, based on their vertical distribution, our findings indicate that in the northern Baltic Sea photoautotrophy (irrespective of the origin of the plastids; cf. Park et al. 2006, Garcia-Cuetos et al. 2010) is the primary mode of nutrition for *D. acuminata*, and that *D. norvegica* may utilize photoautotrophy to a greater extent than lately suggested (Carpenter et al. 1995, Gisselson et al. 2002, Carvalho et al. 2008). This study (study IV), while leaving many of the mysteries surrounding the occurrence of *D. acuminata* and *D. norvegica* unveiled, emphasizes the importance of accurate species determinations and the folly of drawing conclusions on one species based on findings regarding a close relative; even closely associated species may "behave" differently and occupy different ecological niches. It also underlines the importance of complementing long-term (integrated) surface layer investigations (cf. studies I–III) with studies of phytoplankton vertical distributions (cf. study IV) in order to promote the understanding of biotic and abiotic pressures affecting individual species and the phytoplankton community.

6.   CONCLUSIONS

The aim of this thesis was to provide new information on the occurrence of dinoflagellates in the open northern Baltic Sea. We present insights into the ecology (studies I–IV), diversity (studies II–III, this thesis A–B), and spatial and temporal distribution (studies I–IV) of dinoflagellates in the northern Baltic Sea. Below the main contribution of studies I–IV to science and their roles in this thesis are summarized.

- Study I provides new information on how the northern Baltic Sea phytoplankton community of the early 1900s differs from that of today. The most obvious differences were the increase of dinoflagellates and decrease in the diatom to dinoflagellate ratio. To the thesis, this study contributes a century-spanning perspective of phytoplankton community changes, and highlights the importance of dinoflagellates as members of the phytoplankton community.

- Study I shows that it is possible to extract information from historical phytoplankton data and to compare it with modern data, provided that caution is exercised in the selection of datasets and the interpretation of results. Based on the experience gained from this study, I recommend that the feasibility of comparing historical and modern phytoplankton communities also regarding the other sea areas covered by the ICES sampling campaigns be investigated.

- Study II and this thesis provide new information on the diversity and the

spatial and temporal distribution of dinoflagellates in the northern Baltic Sea. On an annual scale, temperature in combination with season is the best predictor of dinoflagellate species composition. Fifteen of the observed 47 species-level taxa have previously not been recorded from the northern Baltic proper and/or the Gulf of Finland. This study complements study I by encompassing a larger number of dinoflagellate taxa and environmental parameters, as well as covering a greater part of the annual cycle.

- Studies I–II show that dinoflagellate occurrence varies both in centurial (study I) and decadal (study II) time frames.

- In study III we describe to science a previously unknown dinoflagellate, *Heterocapsa arctica* subsp. *frigida*, which furthermore represents an unusual taxonomical level for phytoplankton, i.e. a subspecies. This, the only genuinely taxonomical study in this thesis, provides an example of how long-term monitoring and more sophisticated methods can successfully be combined in the study of dinoflagellate diversity.

- Studies I–III demonstrate the applicability of semi-quantitative species data in investigating the phytoplankton community and the occurrence of individual taxa. Based on the experience gained from these studies, I strongly recommend the utilization of the high-quality, high-quantity, semi-quantitative Algaline species data for investigation of the Baltic Sea phytoplankton community.

- Study IV provides information on the ecology of the commonly occurring toxic dinoflagellates *Dinophysis acuminata* and *D. norvegica*, and emphasizes the importance of species-level determination of the phytoplankton community composition.

- Study IV provides a case study example of the vertical distribution of dinoflagellates in the water column, complementing studies I–III in which we investigated (integrated) surface layer sample data.

7. ACKNOWLEDGEMENTS

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Appendix 1. Taxonomical, nomenclatural, and identification-related annotations to the dinoflagellate taxa observed within the framework of this thesis.

Prorocentrum micans
The species concept of *Prorocentrum micans* is not entirely clear. According to some authors, *P. micans* is a highly variable species occurring in a variety of shapes, including roundish short and wide cells with a short and wide spine (e.g. Fukuyo et al. 1990, Bérard-Therriault et al. 1999). In the northern Baltic Sea, the cells of *P. micans* tend to be shorter and wider in proportion than typical *P. micans* in the southern Baltic Sea (G. Hällfors 2004), but this is not always the case; typical slim and long-spined *P. micans* cells have been observed at least as far north as off Helsinki (authors' own observations).

Prorocentrum minimum
Prorocentrum minimum is considered to be conspecific with *P. cordatum* (Ostenfeld) Dodge; the latter has nomenclatural priority (Velikova & Larsen 1999). To date however few authors, e.g. Hoppenrath et al. (2009) and Taylor et al. (2003), have adopted the name *P. cordatum*. The widespread use of the name *P. minimum* in literature from the Baltic Sea and elsewhere would likely justify the conservation of this name.

Amphidinium, Gymnodinium, and Gyrodinium
The gymnodinioid genera *Gymnodinium* F. Stein emend. G. Hansen & Moestrup and *Gyrodinium* Kofoid & Swezy emend. G. Hansen & Moestrup (in Daugbjerg et al. 2000), as well as *Amphidinium* Claparède & Lachmann emend. Flø Jørgensen, Murray & Daugbjerg (in Flø Jørgensen et al. 2004), were recently redefined and new related genera were erected based on ultrastructural characteristics that cannot be distinguished with the conventional methods utilized within phytoplankton monitoring (i.e. light microscopic analysis of acid Lugol's preserved samples; HELCOM 2011). For the purposes of studies such as these (study II, this thesis A–B), it is practical to roughly classify the gymnodinioid dinoflagellates that cannot be identified to species level according to the traditional genus concept based on the relative position and displacement of the cingulum (for traditional genus delimitations see e.g. Hoppenrath et al. 2009).

Gymnodinium and Glenodinium
The delimitation between *Gymnodinium* and *Glenodinium* is not always clear: small- to medium-sized gymnodinioid dinoflagellates may when fixed with acid Lugol's solution appear to possess a thin theca (authors' own observations of cultured specimens). See also below.

Gyrodinium spirale
Gyrodinium spirale is a variable species (Hoppenrath et al. 2009). According Hoppenrath and co-workers (2009), *G. britannicum* Kofoid & Swezy is a very similar species, differentiated only by the number of striae on the cell surface; a feature which is not always easily distinguished in acid Lugol's preserved samples. *Gyrodinium britannicum* occurs as a rare species in the North Sea (Hoppenrath et al. 2009), and has not been recorded from the Baltic Sea (G. Hällfors 2004). While refraining from taking a stand on whether variation in striation is a valid species-specific characteristic [cf. *Sclerodinium* (*Gyrodinium*) *calyptoglyphe* and *S. striatum*; Hoppenrath et al. (2009)], it is possible that specimens of the *G. britannicum*-type have been identified as *G. spirale* in the Baltic Sea.

Glenodinium

The genus *Glenodinium*, which includes species with a thin theca and insufficiently known thecal plate pattern, requires taxonomical reinvestigation (G. Hällfors 2004). Here, we used *Glenodinium* for oval dinoflagellates with a thin, smooth theca, median cingulum and no particular distinguishing features (cf. Tikkanen & Willén 1992: 85, fig. 1–3), in order to distinguish this common type from other unidentified thecate dinoflagellates. See also above.

Oblea rotunda and O. rotunda complex

The *Oblea rotunda* complex comprises *O. rotunda*-like individuals lacking the dictinctive sulcal flange.

Scrippsiella/Biecheleria/Gymnodinium complex

The *Scrippsiella/Biecheleria/Gymnodinium* complex sensu Sundström et al. (2010), the medium-sized, single-celled, ovoid members of which previously were identified as e.g. *Glenodinium* sp., *Gymnodinium* sp., *Peridinium* sp., or *Scrippsiella hangoei* (cf. Sundström et al. 2009), constitutes the three species *Scrippsiella hangoei* (Schiller) Larsen (Larsen et al. 1995), *Biecheleria baltica* Moestrup, Lindberg & Daugbjerg (Moestrup et al. 2009), and *Gymnodinium corollarium* A.M. Sundström, Kremp & Daugbjerg (Sundström et al. 2009), which cannot unambiguously be separated with the methods used in routine phytoplankton monitoring. Also termed *Scrippsiella* complex (Jaanus 2011); not to be confused with the *Scrippsiella*-group sensu Hoppenrath et al. (2009). Members of the complex belong to different orders, here placed under Peridiniales according to the affiliation of *S. hangoei*, the first species described in the complex.

Scrippsiella trochoidea

Scrippsiella trochoidea is easily confused with other species of this genus (*S. hangoei* excluded), as well as members of the genera *Ensiculifera* Balech, *Pentapharsodinium* Indelicato & Loeblich III, and *Calciodinellum* Deflandre, which can be separated only by details in their tabulation and/or cyst morphology (Hoppenrath et al. 2009). None of these other taxa have been recorded east of the Kattegat and Belt Sea area (G. Hällfors 2004). Hoppenrath et al. (2009) refer to these dinoflagellates as the *Scrippsiella*-group, not to be confused with the *Scrippsiella* complex sensu Jaanus (2011), meaning the *Scrippsiella/Biecheleria/Gymnodinium* complex sensu Sundström et al. (2010).

Alexandrium ostenfeldii

Alexandrium ostenfeldii is the only member of this genus that has been recorded from the northern parts of the Baltic Sea (G. Hällfors 2004). An examination of thecal plates, requisite for certain species identification, was however not performed.

Amylax triacantha

The genus *Amylax* comprises the two morphologically very similar species *A. buxus* (Balech) Dodge and *A. triacantha*, their main difference being in the possession of either one (*A. buxus*) or two to several (*A. triacantha*) antapical spines (Hoppenrath et al. 2009). Not all authors consider these to be separate species (cf. Hoppenrath et al. 2009). *Amylax buxus* has not been determined from the Baltic Sea (G. Hällfors 2004). Here, the cells determined as *A. triacantha* are morphologically very variable, and specimens varying from robust and multi-spined to smaller, more delicate with fewer spines, sometimes only the one spine, have been found (author's own observations). The latter probably represent the *A. buxus*-type;

however in the present study, all cells were recorded as *A. triacantha*.

Gonyaulax spinifera

The dinoflagellate known as *Gonyaulax spinifera* comprises several species (e.g. Ellegaard et al. 2002, cf. Hoppenrath et al. 2009), the vegetative stages of which cannot be separated by routine light microscopic analysis. The species are differentiated based on cyst morphology as well as details in vegetative cell-surface ornamentation, cingulum displacement, and number of antapical spines (features which are variable and overlapping between species; Ellegaard et al. 2002). Of the recently described species similar to *G. spinifera,* at least *G. baltica* Ellegaard, Lewis & Harding occurs in the Baltic Sea, based on cyst findings (Ellegaard et al. 2002 and references therein).

Neoceratium tripos

Recently the genus *Ceratium* was split into two genera based on thecal plate pattern and phylogenetic analyses (SSU rDNA) (Gómez et al. 2010). The freshwater species retained the name *Ceratium* while all marine species, among them *C. tripos*, were transferred to the newly erected genus *Neoceratium* F. Gómez, D. Moreira & P. López-Garcia (Gómez et al. 2010). The nomenclatural validity of the name *Neoceratium*, as well as the validity of the transfer of some species into this genus, has been disputed (Calado & Huisman 2010, but see Gómez 2010). The grounds for the split however are well justified (Gómez et al. 2010); based on this I adopt the new name, while acknowledging the importance of correct nomenclatural procedure underlined by Calado & Huisman (2010).

Peridiniella danica

Okolodkov & Dodge (1995) redescribed *Glenodinium danicum* Paulsen as *Peridiniella danica* (Paulsen) Okolodkov & Dodge. However, according to G. Hällfors (2004) the two are not conspecific. Based on the characteristics discernible with light microscopy, the dinoflagellate observed by us fits the description of *P. danica* sensu Okolodkov & Dodge. Neither *P. danica* nor *G. danicum* have previously been reported from the northern Baltic Sea (cf. G. Hällfors 2004).

Pyrophacus horologium

The species name of *Pyrophacus horologium* Stein (see von Stein 1883) is commonly misspelled *horologicum*, as pointed out by Hoppenrath et al. (2009).

Polarella glacialis

Polarella glacialis Montresor, Procaccini & Stoecker was identified based on its cyst, which is very characteristic (cf. Montresor et al. 2003b). The actual vegetative cell is a nondescript gymnodinioid and hardly identifiable with light microscopy (Montresor et al. 1999, 2003b). Investigating 18S rRNA gene diversity in the northern Baltic Sea, Majaneva et al. (2012) found sequences with 100 % match for *P. glacialis* from the Bothnian Bay; ours is the first observation of this species in the northern Baltic proper and the Gulf of Finland.

Thecate dinoflagellates spp.

Thecate dinoflagellates spp. comprise unidentified dinoflagellates other than the *Glenodinium*-type (see above).