

Can *Cylindrospermopsis raciborskii* invade the Baltic Sea?

Jonna Engström-Öst, Ivana Savatijevic Rasic, Andreas Brutemark, Romi Rancken, Gordana Subakov Simić, and Ane T. Laugen

Abstract: Management actions against invasive species are usually most efficient during early stages of invasion. Monitoring for early detection is therefore part of many management plans. However, if monitoring efforts do not match suitable habitat areas, detecting the initial stages of an invasion may fail. We highlight this mismatch by assessing which areas have suitable habitats for an invasion of the cyanobacterium *Cylindrospermopsis raciborskii* in the Baltic Sea, and compare these with the areas that are currently monitored for algal blooms. Establishment of this potential toxin-producer in the Baltic Sea could have serious socio-economic consequences for tourism and recreation, as well as fisheries and aquaculture in the coastal regions. We estimate the coastal areas of the eastern Gulf of Finland as the most suitable area for establishment because of low salinity and high summer seawater surface temperatures. The species is not yet reported in the Baltic Sea, but in the suitable-habitat areas indicated by our assessment, very little monitoring is currently being done. We suggest several lines of research and monitoring to increase the probability of early detection and better predictions for the future distribution of the species.

Key words: cyanobacterium, toxin, climate change, temperature, salinity, Gulf of Finland.

Résumé : Les mesures de gestion contre les espèces invasives sont généralement plus efficaces durant les premiers stades de l'invasion. La surveillance des premières apparitions fait donc partie de nombreux plans de gestion. Cependant, si les efforts de surveillance ne correspondent pas aux habitats convenables, détecter les phases initiales d'une invasion peut échouer. Nous soulignons cette disparité en évaluant quelles zones ont des habitats convenables pour une invasion de la cyanobactérie *Cylindrospermopsis raciborskii* dans la Mer Baltique, et de les comparer avec les zones qui sont actuellement surveillées pour les blooms algaux. L'établissement de ce producteur potentiel de toxine dans la Mer Baltique pourrait avoir de graves conséquences socio-économiques sur le tourisme et les loisirs, ainsi que la pêche et l'aquaculture dans les régions côtières. Nous estimons les zones côtières de l'est du Golfe de la Finlande comme étant celles les plus appropriées pour l'établissement, en raison de la faible salinité et des températures estivales de surface élevées. Les espèces ne sont pas encore signalées dans la Mer Baltique, mais peu de suivi est actuellement effectué dans les habitats convenables signalés par notre étude. Nous suggérons plusieurs pistes de recherche et de surveillance pour augmenter la probabilité de détection précoce et de meilleures prévisions pour la distribution future de l'espèce.

Mots-clés : cyanobactérie, toxine, changement climatique, température, salinité, Golfe de Finlande.

Introduction

Invasive plants and animals are major factors contributing to global biodiversity loss, and their impact can degrade entire ecosystems (Simberloff 2011; Vilà et al. 2011). Ongoing global warming can lead to geographic shifts in suitable habitats, and many tropical or subtropical species are currently expanding their distribution into temperate zones (reviewed by Parmesan 2006). The rufous hummingbird (Hill et al. 1998), tropical dragonflies (Paulson 2001), and the plain tiger butterfly (Haeger 1999) are just a few examples of these occurring shifts. This change is particularly prominent in marine environments where species distributions are moving toward the poles 12 times faster than that of terrestrial species (Poloczanska et al. 2013). For instance, marine organisms such as fish, crustaceans, and micro- and macro-algae shift their habitats northwards due to warmer waters at higher

latitudes (Beaugrand et al. 2002; Hays et al. 2005). Together with biological invasions and larger geographical ranges, climate-induced changes can significantly alter species communities in marginal seas.

One such example is the Baltic Sea, which is a shallow semi-enclosed brackish water basin, with a restricted connection to the North Sea via the Danish straits. The large catchment area leads to a positive freshwater balance, and together with its mean water depth of merely 54 meters make this marginal sea particularly vulnerable to predicted climate-driven changes in abiotic factors. Functionally, the Baltic Sea is a large estuary with both horizontal and vertical salinity gradients. Generally, decreasing salinities are both observed (Raudsepp 2001; Suikkanen et al. 2007, 2013) and forecast (Neumann et al. 2012), because of increasing freshwater run-off from precipitation (Graham 2004) and reduced saltwater

Received 2 September 2014. Accepted 20 January 2015.

J. Engström-Öst. Aronia Coastal Zone Research Team, Novia University of Applied Sciences & Åbo Akademi University, Raseborgsvägen 9, FI-10600 Ekenäs, Finland.

I.S. Rasic. Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, SE-75007 Uppsala, Sweden.

A. Brutemark. Aronia Coastal Zone Research Team, Novia University of Applied Sciences & Åbo Akademi University, Raseborgsvägen 9, FI-10600 Ekenäs, Finland; Tvärminne Zoological Station, University of Helsinki, J.A. Palménin väg 260, FI-10900 Hangö, Finland; Calluna AB, Stockholm, Sweden.

R. Rancken. Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600 Ekenäs, Finland.

G.S. Simić. Faculty of Biology, University of Belgrade, Studentski trg 16, RS-11000 Belgrade, Serbia.

A.T. Laugen. Aronia Coastal Zone Research Team, Novia University of Applied Sciences & Åbo Akademi University, Raseborgsvägen 9, FI-10600 Ekenäs, Finland; Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden.

Corresponding author: Jonna Engström-Öst (e-mail: jonna.engstrom-ost@novia.fi).

intrusions from the North Sea forced by the North Atlantic Oscillation (Dippner et al. 2012). Temperature will increase in major parts of the Baltic Sea, with predicted change in species communities (Neumann et al. 2012).

Harmful bloom-forming algae are a diverse group of species that seems to greatly benefit from climate change (Neumann et al. 2012; O'Neil et al. 2012). Climate change is considered as a catalyst for a global expansion of cyanobacteria (Paerl and Scott 2010; Paerl and Otten 2013), a group of photosynthetic prokaryotes. Cyanobacteria have higher optimal growth temperatures than other microalgae, and thrive in warm, stratified, and nutrient-rich waters (Paerl and Huisman 2009). Lürling et al. (2013) suggest that the estimated future intensification of cyanobacterial blooms caused by warming might not occur as a result of higher growth rates of cyanobacteria compared with their chlorophyte competitors. The competitive advantage of cyanobacteria is more likely due to their resistance to grazing and to their ability to adjust their position in the water column, when climate-induced stratification increases (Lürling et al. 2013).

One such potential invader is *Cylindrospermopsis raciborskii* (Fig. 1). It is a bloom-forming, potentially toxin-producing cyanobacterium that has expanded globally during recent decades (Sinha et al. 2012). The species can produce the hepatotoxin cylindrospermopsin or the neurotoxin saxitoxin (Ohtani et al. 1992; Lagos et al. 1999; Sinha et al. 2012), both with serious consequences for animal and human health. Socio-economic consequences, such as fouled drinking water and decreasing mussel and fish quality resulting in declined tourism and impaired recreational values (O'Neil et al. 2012, Stewart et al. 2012) are common in areas experiencing severe algal blooms.

Cylindrospermopsis raciborskii has spread from the tropics and subtropics to temperate zones of both hemispheres (Padisák 1997). It also occurs commonly in European countries, such as Austria (Dokulil and Teubner 2000), France (Gugger et al. 2005), Germany (Haande et al. 2008), Greece (Moustaka-Gouni et al. 2006), Hungary (Neilan et al. 2003), Italy (Messineo et al. 2010), Poland (Kokociński et al. 2009), Portugal (Neilan et al. 2003), and Serbia (Cvijan and Fuzinato 2011). The likely mechanisms behind its success appear to be a combination of wide physiological tolerance and general climate-related warming (Briand et al. 2004, Bonilla et al. 2012). The contemporary changes in the Baltic Sea and experimental evidence for moderate salinity tolerance (Moisander et al. 2002) suggest that *C. raciborskii* is a potential future inhabitant of the Baltic Sea.

However, to our knowledge, no reports about its presence in the Baltic Sea exist to date. While this could reflect the true situation, it could also be explained by the fact that phytoplankton sampling is most frequently performed in pelagic areas (Helsinki Commission 2013). In the tropics and subtropics the species regularly occurs in deep stratified lakes, but also shallow areas (Figueredo et al. 2007). However, in temperate zones, it inhabits shallower waters (Padisák 1997). This suggests that, if present, *C. raciborskii* could prefer shallow bays also in the Baltic Sea, and might therefore not be detected by regular phytoplankton monitoring.

Aquatic invasive species are common in shallow waters, especially at ports, river mouths, and in coastal inlets, transmitted mainly by ballast water or sediments (Gollasch and Leppäkoski 2007). Because of its current northward expansion and its potential threats to local ecosystems, ecosystem services, and human health, there is an urgent need to assess the probability for *C. raciborskii* to establish viable populations in the Baltic Sea. This paper reviews current knowledge on *C. raciborskii* invasiveness, assesses its potential to establish in the Baltic Sea in light of current environmental conditions and forecast climate scenarios, and outlines future monitoring and research requirements.

Fig. 1. *Cylindrospermopsis raciborskii* trichomes seen under a microscope. The sample was collected in Serbia, Europe. Photo: Gordana Subakov Simić.



Biology and invasiveness

Nowadays, *C. raciborskii* has a global distribution and has established permanent populations on all continents except Antarctica (Sinha et al. 2012; Sukenik et al. 2012). It was first described in Java, Indonesia, and later observed in Southeast Asia, the Middle East, Latin America, and Oceania (reviewed by Sukenik et al. 2012). The *C. raciborskii* population found in Europe is thought to originate from tropical Africa and was first discovered in Greece in the 1930s (references in Mehnert et al. 2010). After being latent for decades, its range has expanded north- and westwards through Europe.

The global distribution and increasing occurrence of *C. raciborskii* can be attributed to its physiological plasticity and tolerance to a large range of environmental factors. The biology of *C. raciborskii* has been covered extensively elsewhere (e.g., Padisák 1997; Sinha et al. 2012; Sukenik et al. 2012). Here, we review the most important features that could help or hinder an invasion event in the Baltic Sea.

First, *C. raciborskii* has an excellent ability to take up nutrients, such as phosphorus and nitrogen. The species has a high affinity for phosphorus and high storage capacity, which suggests that the species is opportunistic with regard to dissolved inorganic phosphorus (Isvánovics et al. 2000, Posselt et al. 2009). It can also switch between using available dissolved inorganic nitrogen and nitrogen fixation, a process that converts relatively inert atmospheric nitrogen (N_2) to ammonium (NH_4) from which N-atoms can be more readily used for biological processes, allowing it to exploit the most energy favorable nitrogen source when available (Burford et al. 2006; Moisander et al. 2012). Tolerance to low availability of nitrogen and phosphorus has been an important factor for the establishment of *C. raciborskii* in European watersheds (Sinha et al. 2012). In the Baltic Sea, summertime levels of nitrogen and phosphorus are low (Table 1) due to efficient uptake by microalgae (Suikkanen et al. 2007), and the relatively effective uptake of these compounds by *C. raciborskii* increases its competitiveness.

Second is its shade tolerance (Pádisák and Reynolds 1998; Briand et al. 2004), which increases its competitiveness in highly turbid water. The Baltic Sea water is turbid (Table 1), shown by decreasing Secchi depths during the last century (Fleming-Lehtinen and Laamanen 2012), and its ability to grow in low light will facilitate its existence under such conditions (eu-photic depth ~10 m; Raateoja et al. 2004).

Table 1. Background information on the current state in the Gulf of Finland and in tropical lakes (where *Cylindrospermopsis raciborskii* is established). Gulf of Finland was selected as the area suggested to be the most suitable habitat for *C. raciborskii* in the Baltic Sea.

Baltic Sea	Mean	Range (min.–max.)	Mean (1970s)	Tropical and subtropical lakes mean [‡] (range: min.–max.)
Temperature*	19 °C	18–20 °C	15 °C	25.7 °C (11.2–31.6 °C)
Salinity [†]	4.9	4.6–5.3	5.3	Not reported
pH [‡]	8.05	7.7–8.5	8.4	8.2 (5.49–9.91)
Nitrogen*	8 µmol L ⁻¹	7–9 µmol L ⁻¹	5 µmol L ⁻¹	Not reported
Phosphorus*	1 µmol L ⁻¹	0.75–1.00 µmol L ⁻¹	0.7 µmol L ⁻¹	74.9 µg L ⁻¹ (12.4–658 µg L ⁻¹)
Secchi	5	3–8	9 (mean 1903)	0.68 m (0.09–3.78 m); Z_{eu}/Z_{mix}

Note: Z_{eu}/Z_{mix} , euphotic zone/mixing zone; a proxy of the light available in the environment for phytoplankton growth.

*Suikkanen et al. 2013.

†Suikkanen et al. 2007.

‡Brutemark et al. 2011.

||Fleming-Lehtinen and Laamanen 2012.

‡Review by Bonilla et al. 2012.

Third is its relatively wide thermal tolerance range (Dokulil and Teubner 2000; Briand et al. 2004). Independent of latitude, *C. raciborskii* grows only in warm water (>25 °C), thus often in far higher temperatures than encountered in the Baltic Sea (Table 1). However, it has also been suggested that it gradually adapts to cooler temperatures in more temperate waters. For instance, in the River Danube, Austria, a mass-occurrence of this species was detected in water temperatures of only 15–18 °C (Dokulil and Mayer 1996; Piccini et al. 2011). Although the summer water temperature in the Baltic Sea is gradually increasing (Meier et al. 2012; Suikkanen et al. 2013), the temperature is probably still the main barrier for successful invasion (Table 1; Fig. 2a), even though Bonilla et al. (2012) showed that *C. raciborskii* can grow at 11 °C. Nevertheless, warming does promote *C. raciborskii* advancement northwards in temperate areas (Wiedner et al. 2007), but the native bloom-forming cyanobacteria (such as *Aphanizomenon*) also thrive in warm water and show a positive long-term trend with temperature (Suikkanen et al. 2013).

Fourth is its ability to withstand relatively high salinities (up to salinity 4 in the laboratory; Moisaner et al. 2002). While *C. raciborskii* is predominantly a freshwater species, it has evolved salinity tolerance in environments experiencing periodic drying and salinity flux (Padisák 1997). For instance, in Australian river habitats (Sinha et al. 2012), the Caspian Sea (Padisák 1997), and an estuary in North Carolina, USA (Calandrino and Paerl 2011), the species tolerate salinities up to 2. As discussed in the previous section, the Baltic Sea is a brackish-water basin, ranging from a surface salinity of 7 in the south to ~2 in the north and east (Fig. 2b). Thus, many parts of the Baltic Sea would have low enough salinity to allow for the establishment of *C. raciborskii* and for its potential to displace competitors. On the other hand, occasional major saltwater inflows from the North Atlantic to the Baltic Sea (Dippner et al. 2012) could hinder or slow down an invasion by *C. raciborskii*.

Fifth is its tolerance to high pH. It can be due to a direct pH effect, but since the fraction of CO₂ decreases as pH increases, high pH can result in CO₂ limitation for phytoplankton. As cyanobacteria, including *C. raciborskii*, have the ability to also use other carbon sources, such as HCO₃⁻ (Holland et al. 2012), they are often good competitors at high pH and low CO₂ and can outcompete other phytoplankton (Shapiro 1973). In fact, *C. raciborskii* is often found in lakes with a relatively high pH (>8, Padisák 1997; Bouvy et al. 2000; Briand et al. 2002; 7.0–9.6, Saker et al. 2003). The summertime surface pH in parts of the Baltic Sea fluctuates between 7.5 and 9.2 (Omstedt et al. 2010; Brutemark et al. 2011) and would thereby be suitable for the establishment of *C. raciborskii*.

Sixth is the ability to be planktonic year-round (i.e., holoplanktonic), and not form resting stages. Suikkanen et al. (2010) have suggested that the most successful strategy among bloom-forming cyanobacteria in the Baltic Sea seems to be a holoplank-

tonic lifecycle. This is due to the possibility to form blooms more rapidly when constantly occurring in the water column and not being dependent on resting stages on the sediment (e.g., *Dolichospermum*, prev. *Anabaena*). *Aphanizomenon flos-aquae* is holoplanktonic and dominates the cyanobacterial biomass in the Baltic Sea. *Cylindrospermopsis raciborskii* is also holoplanktonic (Saker and Griffiths 2000), which suggests it could be a strong competitor to *A. flos-aquae*. *Cylindrospermopsis raciborskii* possesses the ability to form akinetes, but rarely uses this strategy in the wild (Everson et al. 2011 and references therein). Akinete formation is strongly temperature-dependent (Alster et al. 2010) and *C. raciborskii* would probably behave differently in the Baltic Sea than in the subtropics, as akinetes provide resistance to unfavorable environments (Everson et al. 2011).

Seventh is its resistance to grazing due to morphological characters, such as filaments, and toxicity (Table 1; Leonard and Paerl 2005; Hong et al. 2013). It has been shown that *C. raciborskii* can be highly toxic in cooler waters (Everson et al. 2011), suggesting that toxin production is not always positively correlated with warming.

Eighth is its possible allelopathic capabilities that inhibit growth of other phyto- or bacterioplankton (Figueredo et al. 2007). All these are factors that may favor establishment and proliferation of *C. raciborskii* in the Baltic Sea. These factors are discussed in more detail below. In the next section, we will review current knowledge on vectors that could introduce *C. raciborskii* to the Baltic Sea.

Potential dispersal vectors

Many invasion biologists have classified the different stages that invasive species undergo when expanding their ranges to new areas. Theoharides and Dukes (2007) identify four main stages of invasion: introduction, naturalization, colonization, and dispersal (Table 2). In Table 2, we present the biotic and abiotic factors that would be the most relevant for evaluating the potential of *C. raciborskii* to invade the Baltic Sea.

Species movements have always occurred, but current unintentional movements of species are happening faster as a consequence of global commerce and travel (reviewed by Theoharides and Dukes 2007). To pass the first stage of invasion (introduction, Table 2) *C. raciborskii* could be introduced in the Baltic Sea in multiple ways. Wind transport is an efficient means to transfer microorganisms, prokaryotes, and protists (Smith et al. 2011), but the two most likely vectors are either by birds or through human activities (Padisák 1997). The former may occur when migratory water birds pick up the cyanobacterium in the overwinter areas in the tropics or at European stopover lakes, and deposit this species during subsequent stops in the Baltic Sea. Birds have probably transferred the species from the site where it was first described

Fig. 2. Map of the Baltic Sea showing average sea surface temperature (a) and salinity (b) between 15 July and 15 August 2003–2013 from surface to 5 m depth. The data was extrapolated from database Sumppu, using dataware Grafeo. Data were obtained from the Finnish Meteorological Institute (www.fmi.fi). We produced the maps in ArcGIS Spatial Analyst combining a basemap from ESRI Data and Maps 2006 with interpolated environmental data. To interpolate the environmental data between the measurement stations, we used the tool Spline with Barriers where the continental coastline is used as barrier. Smoothing factor was set to 0.

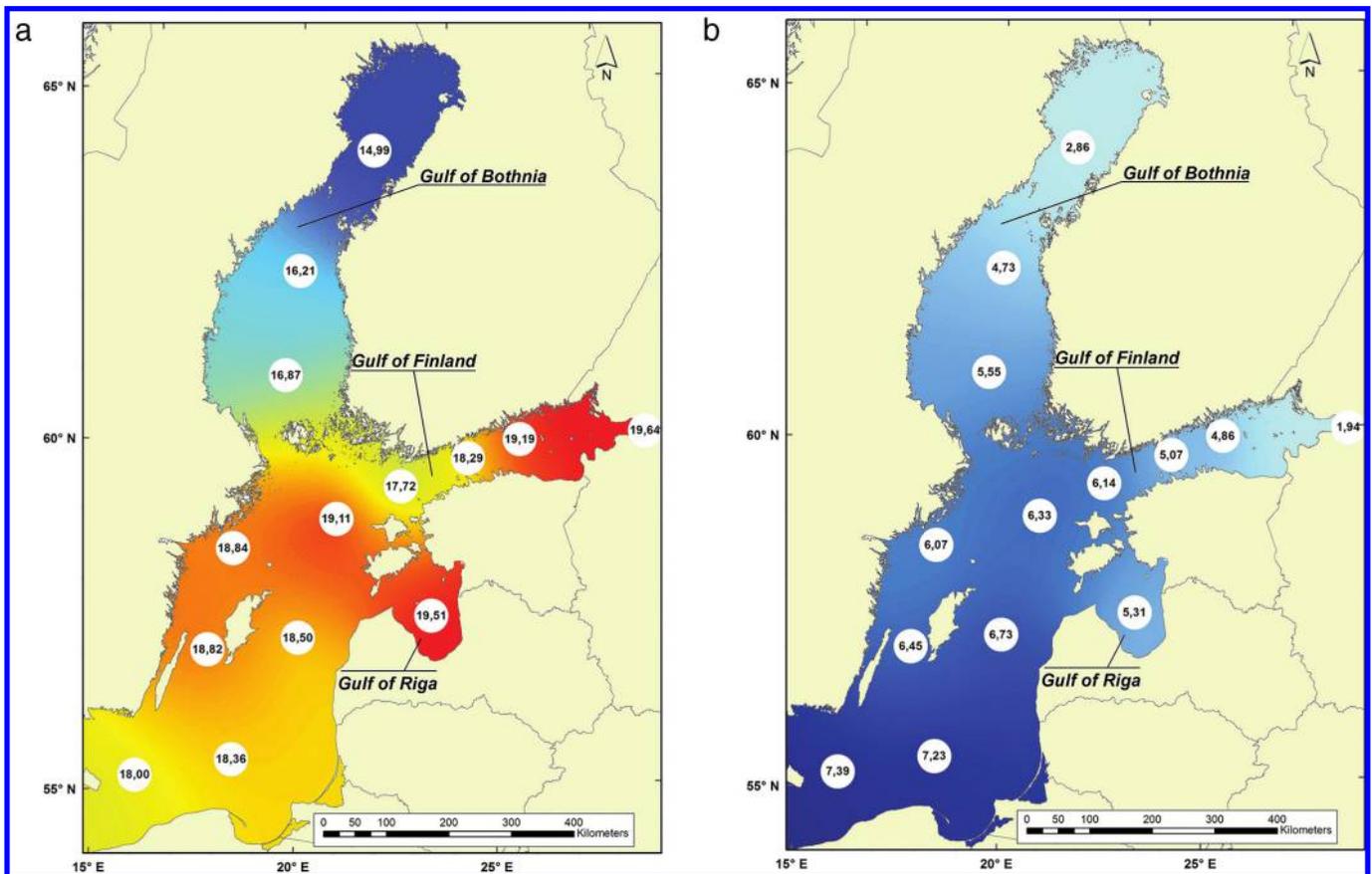


Table 2. Four stages of invasion, major filters, definition of stage, and specific characteristics of *Cylindrospermopsis raciborskii* for each stage (modified after Theoharides and Dukes 2007).

Stage	General filters	Specific for <i>C. raciborskii</i>
Introduction Transported species become common in an area	Geographic distance and barriers to long-distance dispersal (waterbodies, deserts, mountains)	Fishing gear, water birds, boating, river outflow, ballast water
Naturalization Abiotic factors determine whether an introduced species can survive and reproduce in the new habitat	Abiotic barriers to colonization	<ul style="list-style-type: none"> • Temperature: 25–30 °C; winter: 15 °C • Salinity: 1.5–2 • pH: 8–8.7 • Light: tolerate 0.5–500 mmol photons m⁻² s⁻¹, optimal: 30 mmol photons m⁻² s⁻¹ • Nitrogen: grow better with NO₃⁻ or NH₄⁺ than N fixation • Phosphorus: high affinity and storage capacity • Water column stability: dominate in shallow mixed systems
Colonization Native species create biotic resistance to establishment by suppressing reproductive rates, outcompeting the alien species through fast growth and efficient resource use	Biotic filters to population growth and establishment	Pathogens (cyanophags), competitors (other phytoplankton), herbivores, (grazers), lack of mutualists (local bacteria), allelopathic or toxic ability (kills or deactivate competitors or grazers); grazers can cut/shorten filaments
Dispersal Dispersal rates depend on dispersal ability, possible dispersal vectors, and habitat connectivity	Landscape filters to dispersal and establishment in new areas	Akinete formation, tolerance to low availability of P and N, relatively high salt tolerance, Baltic Sea water currents, high shipping activity

in Java to other continents (Padisák 1997). Human activities known to unintentionally introduce alien species include ship traffic and transferring dirty fishing gear from infected to uninfected localities. It is, however, unclear which vector may be most probable for the transport of *C. raciborskii*, as this species prefers habitats, such as smaller ponds and lakes, where shipping is negligible. In the following section, we will assess which areas in the Baltic Sea that are most susceptible to a *C. raciborskii* invasion and which factors could prevent establishment of the species.

Potential hotspots for *C. raciborskii* in the Baltic Sea

Figures 2a and 2b present the late summer mean surface seawater temperatures and surface seawater salinity, respectively, in the Baltic Sea over the last 10 years. Evaluating these two variables in isolation, the maps suggest that the eastern Gulf of Finland provides the most beneficial circumstances for a potential *C. raciborskii* establishment. The seawater in the eastern Gulf of Finland reaches high temperature (up to 20 °C during summer; Fig. 2a), partly because the bay is shallow (inner bay < 20 m) and partly because it is sheltered from storms (Pitkänen et al. 1993). Additionally, the area seldom receives the occasional saline deep-water inflows from the southern Baltic Sea, so the water surface salinity is almost fresh (inner bay ~1‰). The River Neva also brings large amounts of freshwater to the area (Pitkänen et al. 1993). The inflowing water is also fairly enriched in nutrients. Although sewage treatment has improved considerably as of late, the eutrophication status off St. Petersburg in the eastern Gulf of Finland still has the status level “bad” according to Helsinki Commission (2013). The majority of the basins in the Baltic Sea has either status level “poor” or “bad” (Helsinki Commission 2013), indicating that the Baltic Sea still has a serious problem with eutrophication. A shade-tolerant species, such as *C. raciborskii*, may nonetheless thrive in these waters. Since the temperature in the eastern Gulf of Finland is clearly high enough for *C. raciborskii* to survive, it remains unknown whether the species can evolve the capacity to reproduce efficiently enough to definitively pass the second stage of invasion (Table 2).

The thermal conditions in the Gulf of Riga also seem beneficial for this species; the temperature in the area reaches similar levels (19–20 °C) as in the eastern Gulf of Finland (Fig. 2a). However, surface seawater salinity is generally higher in this area. The mean surface seawater salinity in the Gulf of Riga normally varies between 4.5 and 8, but the average salinity increases during weak river flow and decreases during strong river flow (Raudsepp 2001). According to Reichwaldt and Ghadouani (2012), the rainfall in northern Europe will likely increase in the future, and Meier et al. (2012) have predicted a decrease in the Baltic Sea surface and bottom salinity regimes. It is therefore possible that the Gulf of Riga in the future will provide suitable *C. raciborskii* habitats.

In the Bothnian Bay, the salinity regime would probably be favorable for *C. raciborskii*, but we consider the thermal conditions too cold for this species to enable efficient growth. Everson et al. (2011) report that peak cell concentrations of *C. raciborskii* occurred in the water column when surface water temperatures were 19.1 °C (cf. Figure 2a). However, the Bothnian Bay is not expected to attain such high mean sea surface temperature in the near future despite a predicted two- to three-fold increase in probability of sea surface temperature reaching 18 °C in central areas of the Baltic Sea (Neumann et al. 2012).

The main constraining factor for *C. raciborskii* survival and reproduction in the Baltic Sea is very likely low winter temperatures that are close to 4 °C throughout the water column. A prerequisite for algal persistence in a temperate or Arctic environment is a successful over-winter strategy, such as the low-temperature tolerance in filamentous cyanobacteria in Antarctica, e.g., *Aphanotocece*, *Chroococcus*, *Oscillatoria*, and *Phormidium* (McKnight et al. 2000). *Cylindrospermopsis raciborskii* resting stages can also survive unfav-

orable conditions in sediments for long periods of time (Everson et al. 2011), as the species has established populations in North America including in Lake Winnipeg, and Lake Erie (Sukenik et al. 2012 and references therein), which suggests that low winter temperatures are not necessarily a limitation for this species.

Cylindrospermopsis raciborskii thrives in strongly stratified environments (no water-layer mixing; Padisák 1997), as water-column stability promotes cyanobacterial biomass (Jöhnk et al. 2008; Taranu et al. 2012). *Cylindrospermopsis raciborskii* may be unable to establish persistent populations in open-sea areas if the increasing trend of climate-induced storm frequency persists in Scandinavia (Neumann 2010). However, shallow, more sheltered areas in coastal regions may escape more of the storm-induced mixing and thereby provide refuge for the species.

Biotic interactions

The success of an invader does not rely on the suitability of abiotic factors alone. On the contrary, biotic interactions may play a vital role in determining the speed of settlement and the degree of impact on the local environment. In the case of invading cyanobacteria, such as *C. raciborskii*, the interaction between cyanobacteria and heterotrophic bacteria can be both mutually detrimental (e.g., competition and antibiotic effects; reviewed by Legrand et al. 2003) or beneficial, such as excretion of organic compounds that bacteria can utilize whilst they remineralize nutrients for primary producers (reviewed by Cole 1982). Examples of community-level mutually beneficial effects include higher bacteria abundance during a *C. raciborskii* bloom due to increased levels of organic matter for bacterial growth (Bouvy et al. 2001), and boosted *C. raciborskii* growth due to bacterial presence (Bagatini et al. 2014).

As stated above, *C. raciborskii* is characterized as an ecologist using facultative diazotrophy, i.e., optional N-fixation (Mur et al. 1999, Dokulil and Teubner 2000). As the surface waters of the open Baltic Sea in late summer are nitrogen-depleted, it supports the growth of nitrogen-fixing cyanobacteria (Sivonen et al. 2007), indicating that the ability to fix nitrogen is essential in the competition with other cyanobacteria. *Cylindrospermopsis raciborskii* can also gain a growth advantage (in relation to *A. flos-aquae*, the main bloom-forming species in the Baltic Sea) under fluctuating dissolved inorganic nitrogen conditions (Moisander et al. 2012), as *C. raciborskii* is able to grow in both mixed (Dokulil and Teubner 2000) and stable waters (Padisák 1997). In mixed waters, *A. flos-aquae* gains a benefit over *Nodularia spumigena*, whereas it is out-competed by *N. spumigena* due to its higher N-fixation by the species in stable waters (Stal et al. 2003). In batch culture studies, *N. spumigena* preferred warm temperatures and high irradiances, whereas *A. flos-aquae* preferred colder temperatures, lower salinities, and irradiances (reviewed by Sivonen et al. 2007). *Cylindrospermopsis raciborskii* prefers warm temperatures and low salinities (Sinha et al. 2012) and therefore it is unlikely to share habitats with *N. spumigena*. Another key species, *Planktothrix*, prefers stable waters and cooler temperatures and could be an important competitor to *C. raciborskii*, if *C. raciborskii* becomes successfully established in the Baltic Sea. Similarly, *Microcystis* prefers freshwater and occurs only in the eastern Gulf of Finland and the Curonian Lagoon in the Baltic Sea area (Belykh et al. 2013), and is therefore an important potential competitor with *C. raciborskii*. *Cylindrospermopsis raciborskii* can, given the right circumstances (such as light and dissolved inorganic nitrogen, especially NH₄⁺) outcompete *Anabaena* (Moisander et al. 2008), *Aphanizomenon* (Wu et al. 2009; Mehnert et al. 2010), *Microcystis* (Wu et al. 2009; Mello et al. 2012; Rzymiski et al. 2014), and *Planktothrix* (Kokociński et al. 2010, Bonilla et al. 2012, Ammar et al. 2014).

In terms of grazing, both copepods and rotifers feed upon straight and coiled cyanobacterial filaments under laboratory conditions (Kå et al. 2012). Moreover, copepods are likely able to cut and shorten these filaments (Bouvy et al. 2001), thereby increasing the availability

for cladocerans. Despite possibly being used as prey in some cases, *C. raciborskii* persistence might primarily be promoted by copepods preferentially grazing on other algae (Hong et al. 2013), indicating a significant loss of top-down control of invasiveness and blooms as *C. raciborskii* abundance increases. Baltic copepods, such as *Acartia* and *Eurytemora* that constitute potential grazers of *C. raciborskii* seem fairly resistant to cyanobacterial toxins (Reinikainen et al. 2002). There is little knowledge available on the joint effect of different cyanobacteria toxins on higher trophic levels.

Further up in trophic levels, *C. raciborskii* toxicity may influence mortality and increased liver toxin concentrations in fish during strong *C. raciborskii* blooms (Chellappa et al. 2008). These effects may, however, depend on the life stage at which exposure occurs. While adult zebrafish seem to be quite tolerant to *C. raciborskii* toxicity, exposure at the larval stages induce increased mortality (Zagatto et al. 2012). Also, Baltic Sea fish could be affected by *C. raciborskii* toxins as they are proven sensitive to cyanobacterial toxins (Kankaanpää et al. 2001). In the next section, we will discuss the potential of *C. raciborskii* to disperse within the Baltic Sea.

Dispersal potential of *C. raciborskii*

To pass the third stage of invasion, a new species will have to be able to cope with potential biotic resistance in the ecosystem. For *C. raciborskii* this mainly means overcoming allelopathy, the inhibitory effects of plants and microorganisms on other plant species or microorganisms through the release of organic compounds, and grazing pressure (Leflaive and Ten-Hage 2007). Figueredo et al. (2007) demonstrated that *C. raciborskii* caused strong inhibitory effects on the photosynthetic rates of other phytoplankton. The authors suggest that allelopathy could constitute a competitive benefit for the cyanobacterium and enhance its potential to establish new populations, and even provide an explanation for its geographic expansion in mid-latitudes. Thus, it is likely that allelopathic resistance from other species will not be a major obstacle for *C. raciborskii* in the Baltic Sea. However, virtually no research on how *C. raciborskii* may interact with Baltic Sea micro-flora exists, so predictions are difficult to make. Concerning grazing pressure, Hong et al. (2013) showed that selective foraging by copepods facilitated *C. raciborskii* bloom build-up, as the copepods preferred other food, e.g., green algae *Chlamydomonas*. Similarly, Fabbro and Duivenvoorden (1996) reported an absence of copepod grazing upon *C. raciborskii*, whereas Bouvy et al. (2001) reported low edibility of mono-species *C. raciborskii* blooms in Ingazeira reservoir, northeast Brazil.

The fourth stage of invasion concerns dispersal to new areas from the established population (Table 2). If *C. raciborskii* were to establish a population in the eastern Gulf of Finland, its dispersal would be constrained by the salinity regime occurring in the south-western part of the basin (Neumann et al. 2012; Fig. 2b), as well as by the temperature regime in the northern parts of the basin, when dispersing northwards (Fig. 2a). However, the water currents flow in an anti-clockwise direction in the Gulf of Finland, and after a potential establishment in the eastern part of the gulf, currents along the Finnish coast would provide ample possibilities for efficient spatio-temporal movement on a regional scale. The archipelago along the south and south-western coastline of Finland may also harbor locations where favorable conditions for *C. raciborskii* survival and population growth occur regularly.

Future perspectives

The interest in *C. raciborskii* increased substantially after it was first discovered in the developed world. For instance, several reviews on their ever-expanding range distribution and responses to climate change have been published recently (e.g., Briand et al. 2004; Sinha et al. 2012; Sukenik et al. 2012). Above, we have summarized the available knowledge that is relevant to the species in terms of possible establishment in the Baltic Sea. However, sev-

eral knowledge gaps need to be filled before any quantitative predictions can be made. These are especially important for stages one and two described in Table 2 (introduction and naturalization).

First and foremost, we need to establish monitoring schemes for coastal areas where *C. raciborskii* is most likely to appear. Currently, plankton monitoring in the Baltic Sea proceeds in pelagic zones, but according to our analysis above, this sampling scheme will likely not detect any *C. raciborskii* on its way through the first stage of invasion. Rather, monitoring the eastern Gulf of Finland should be a high priority. Early detection of potential invaders is central, to implement efficient management actions before species establishment and colonization. Easy-to-use kits enable the early detection of impending cyanobacterial blooms. The kits are most effective if the effort to distribute them and share information about them is successful (Bartram et al. 1999).

The second stage of invasion requires the ability of *C. raciborskii* to survive and reproduce under contemporary environmental conditions. A first step towards simple quantitative predictions about current and future distribution of range-expanding species is Ecological Niche Modelling (EME; Elith and Leathwick 2009). EME combines data on the global distribution of the focal species with data on important environmental variables to pin-point areas outside the known distribution that may harbour suitable habitats. Moreover, using future climate scenarios EME can also forecast possible future distribution ranges, and is currently being used to predict range expansion of other invasive species (e.g., Lima et al. 2007; Laugen et al. 2015).

Three important limitations with EME and related modelling approaches are (i) that they are purely correlative, (ii) they are not focused on predicting distribution when combinations of environmental factors change, and (iii) they do not take local adaptation and evolutionary response to changing environmental factors into account. Some experimental studies on *C. raciborskii* tolerance to environmental factors, such as temperature, salinity, and light exist (Moisander et al. 2002; Briand et al. 2004; Piccini et al. 2011). However, virtually no studies have examined the evolutionary potential of the strains currently present in central Europe to further northward expansion. A second important step towards quantitative predictions about range expansion in northern Europe should therefore be a research programme focussing on estimating evolutionary potential along several axes of environmental variation, as well as tolerance to multiple environmental stressors. Such data are crucial for developing and parameterizing mechanistic niche models (Kearney et al. 2012), which thoroughly combines the functional traits of organisms with current and future environment.

The invasive cyanobacterium *C. raciborskii* is migrating towards higher latitudes, and has already been observed as close to the Baltic Sea as Poland (Kokociński et al. 2009). We argue that despite this being a predominantly freshwater species, the combination of current environmental factors and the possible negative consequences of the species, make the risk of ignoring this species as a potential invader in the Baltic Sea too high. Thus, we suggest a combination of regular Baltic Sea coastal water monitoring, ecological niche modelling, and experimental evaluation of its tolerance ranges, to detect and predict the future range of *C. raciborskii* in North European waters.

Acknowledgements

We thank the Editor and reviewers for valuable comments on the manuscript. The authors warmly thank Kimmo Tikka at the Finnish Meteorological Institute for the data searches and discussions, Colette Gattoni for correcting the language, and Olivier Glippa for translating the abstract. The study was funded by Norden Havgrupppe, the Walter and Andrée de Nottbeck Foundation, and the Academy of Finland (project No. 276947).

References

Alster, A., Kaplan-Levy, R.N., Sukenik, A., and Zohary, T. 2010. Morphology and phylogeny of a non-toxic invasive *Cylindrospermopsis raciborskii* from a Mediterranean Lake. *Hydrobiologia*, **639**: 115–128. doi:10.1007/s10750-009-0044-y.

Ammar, M., Comte, K., Tran, T.D.C., and El Bour, M. 2014. Initial growth phases of two bloom-forming cyanobacteria (*Cylindrospermopsis raciborskii* and *Planktothrix agardhii*) in monocultures and mixed cultures depending on light and nutrient conditions. *Ann. Limnol. - Int. J. Lim.* **50**: 231–240. doi:10.1051/limn/2014096.

Bagatini, I.L., Eiler, A., Bertilsson, S., Klaveness, D., Tessarolli, L.P., and Vieira, A.A.H. 2014. Host-specificity and dynamics in bacterial communities associated with bloom-forming freshwater phytoplankton. *PLoS One*, **9**: e85950. doi:10.1371/journal.pone.0085950. PMID:24465807.

Bartram, J., Vapnek, J.C., Jones, G., Bowling, L., Falconer, I., and Codd, G.A. 1999. Implementation of management plans. In *Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management*. Edited by I. Chorus and J. Bartram. E&FN Spon, WHO, London, England. pp. 211–231.

Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**: 1692–1694. doi:10.1126/science.1071329. PMID:12040196.

Belykh, O.I., Dmitrieva, O.A., Gladkikh, A.S., and Sorokovikova, E.G. 2013. Identification of toxigenic cyanobacteria of the genus *Microcystis* in the Curonian Lagoon (Baltic Sea). *Oceanology*, **53**: 71–79. doi:10.1134/S0001437013010025.

Bonilla, S., Aubriot, L., Soares, M.C.S., González-Piana, M., Fabre, A., Huszar, V.L.M., et al. 2012. What drives the distribution of the bloom-forming cyanobacteria *Planktothrix agardhii* and *Cylindrospermopsis raciborskii*? *FEMS Microbiol. Ecol.* **79**: 594–607. doi:10.1111/j.1574-6941.2011.01242.x. PMID:22092489.

Bouvy, M., Falcão, D., Marinho, M., Pagano, M., and Moura, A. 2000. Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquat. Microb. Ecol.* **23**: 13–27. doi:10.3354/ame023013.

Bouvy, M., Pagano, M., and Troussellier, M. 2001. Effects of a cyanobacterial bloom (*Cylindrospermopsis raciborskii*) on bacteria and zooplankton communities in Ingazeira reservoir (northeast Brazil). *Aquat. Microb. Ecol.* **25**: 215–227. doi:10.3354/ame025215.

Briand, J.F., Robillot, C., Quiblier-Llobéras, C., Humbert, J.F., Couté, A., and Bernard, C. 2002. Environmental context of *Cylindrospermopsis raciborskii* (Cyanobacteria) blooms in a shallow pond in France. *Water Res.* **36**: 3183–3192. doi:10.1016/S0043-1354(02)00016-7. PMID:12188114.

Briand, J.F., Leboulanger, C., Humbert, J.F., Bernard, C., and Dufour, P. 2004. *Cylindrospermopsis raciborskii* (Cyanobacteria) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming? *J. Phycol.* **40**: 231–238. doi:10.1111/j.1529-8817.2004.03118.x.

Brutemark, A., Engström-Öst, J., and Vehmaa, A. 2011. Long-term monitoring data reveal pH dynamics, trends and variability in the western Gulf of Finland. *Oceanol. Hydrobiol. Stud.* **40**: 91–94. doi:10.2478/s13545-011-0034-3.

Burford, M.A., McNeale, K.L., and McKenzie-Smith, F.J. 2006. The role of nitrogen in promoting the toxic cyanophyte *Cylindrospermopsis raciborskii* in a subtropical water reservoir. *Freshwater Biol.* **51**: 2143–2153. doi:10.1111/j.1365-2427.2006.01630.x.

Calandrino, E.S., and Paerl, H.W. 2011. Determining the potential for the proliferation of the harmful cyanobacterium *Cylindrospermopsis raciborskii* in Currituck Sound, North Carolina. *Harmful Algae* **11**: 1–9. doi:10.1016/j.hal.2011.04.003.

Chellappa, N.T., Chellappa, S.L., and Chellappa, S. 2008. Harmful phytoplankton blooms and fish mortality in a eutrophicated reservoir of northeast Brazil. *Braz. Arch. Biol. Technol.* **51**: 833–841. doi:10.1590/S1516-89132008000400022.

Cole, J.J. 1982. Interactions between bacteria and algae in aquatic ecosystems. *Annu. Rev. Ecol. Syst.* **13**: 291–314. doi:10.1146/annurev.es.13.110182.001451.

Cvijan, M., and Fužinato, S. 2011. The first finding of *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, 1972 (Cyanoprokaryota) in Serbia. *Arch. Biol. Sci.* **63**: 507–510. doi:10.2298/ABS1102507C.

Dippner, J.W., Möller, C., and Hänninen, J. 2012. Regime shifts in North Sea and Baltic Sea: a comparison. *J. Marine Syst.* **105–108**: 115–122. doi:10.1016/j.jmarsys.2012.07.001.

Dokulil, M.T., and Mayer, J. 1996. Population dynamics and photosynthetic rates of a *Cylindrospermopsis-Limnolthrix* association in a highly eutrophic urban lake, Alte Donau, Vienna, Austria. *Algolog. Stud.* **83**: 179–195.

Dokulil, M.T., and Teubner, K. 2000. Cyanobacterial dominance in lakes. *Hydrobiologia*, **438**: 1–12. doi:10.1023/A:1004155810302.

Elith, J., and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* **40**: 677–697. doi:10.1146/annurev.ecolsys.110308.120159.

Everson, S., Fabbro, L., Kinnear, S., and Wright, P. 2011. Extreme differences in alkenete, heterocyte and cylindrospermopsin concentrations with depth in a successive bloom involving *Aphanizomenon ovalisporum* (Forti) and *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Subba Raju. *Harmful Algae*, **10**: 265–276. doi:10.1016/j.hal.2010.10.006.

Fabbro, L.D., and Duivenvoorden, L.J. 1996. Profile of a bloom of the cyanobacterium *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Subba Raju in the Fitzroy River in tropical central Queensland. *Mar. Freshwater Res.* **47**: 685–694. doi:10.1071/MF9960685.

Figueredo, C.C., Gianni, A., and Bird, D.F. 2007. Does allelopathy contribute to *Cylindrospermopsis raciborskii* (Cyanobacteria) bloom occurrence and geographic expansion? *J. Phycol.* **43**: 256–265. doi:10.1111/j.1529-8817.2007.00333.x.

Fleming-Lehtinen, V., and Laamanen, M. 2012. Long-term changes in Secchi depth and the role of phytoplankton in explaining light attenuation in the Baltic Sea. *Estuarine, Coastal Shelf Sci.* **102–103**: 1–10. doi:10.1016/j.ecss.2012.02.015.

Gollasch, S., and Leppäkoski, E. 2007. Risk assessment and management scenarios for ballast water mediated species introductions into the Baltic Sea. *Aquat. Invasions*, **2**: 313–340. doi:10.3391/ai.2007.2.4.3.

Graham, L.P. 2004. Climate change effects on river flow to the Baltic Sea. *AMBIO*, **33**: 235–241. doi:10.1579/0044-7447-33.4.235. PMID:15264602.

Gugger, M., Molica, R., Le Berre, B., Dufour, P., Bernard, C., and Humbert, J.-F. 2005. Genetic diversity of *Cylindrospermopsis* strains (Cyanobacteria) isolated from four continents. *Appl. Environ. Microbiol.* **71**: 1097–1100. doi:10.1128/AEM.71.2.1097-1100.2005. PMID:15691973.

Haande, S., Rohrlack, T., Ballot, A.R., Røberg, K., Skulberg, R., Beck, M., and Wiedner, C. 2008. Genetic characterisation of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) isolates from Africa and Europe. *Harmful Algae*, **7**: 692–701. doi:10.1016/j.hal.2008.02.010.

Haeger, J.F. 1999. *Danaus chrysipus* (Linnaeus, 1758) en la Peninsula Iberica: migraciones o dinimica de metapoblaciones? *Shilap Rev. Lepidop.* **27**: 423–430. [In Spanish.]

Hays, G.C., Richardson, A.J., and Robinson, C. 2005. Climate change and marine plankton. *Trends Ecol. Evol.* **20**: 337–344. doi:10.1016/j.tree.2005.03.004. PMID:16701390.

Helsinki Commission. 2013. Approaches and methods for eutrophication target setting in the Baltic Sea region. *Balt. Sea Environ. Proc.* **133**: 1–134.

Hill, G.E., Sargent, R.R., and Sargent, M.B. 1998. Recent change in the winter distribution of Rufous Hummingbirds. *Auk*, **115**: 240–245. doi:10.2307/4089135.

Holland, D.P., Pantorno, A., Orr, P.T., Stojkovic, S., and Beardall, J. 2012. The impacts of a high CO₂ environment on a bicarbonate user: the cyanobacterium *Cylindrospermopsis raciborskii*. *Water Res.* **46**: 1430–1437. doi:10.1016/j.watres.2011.11.015. PMID:22119367.

Hong, Y., Burford, M.A., Ralph, P.J., Udy, J.W., and Doblin, M.A. 2013. The cyanobacterium *Cylindrospermopsis raciborskii* is facilitated by copepod selective grazing. *Harmful Algae*, **29**: 14–21. doi:10.1016/j.hal.2013.07.003.

Isvánovics, V., Shafik, H.M., Présing, M., and Juhos, S. 2000. Growth and phosphate uptake kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in throughflow cultures. *Freshwater Biol.* **43**: 257–275. doi:10.1046/j.1365-2427.2000.00549.x.

Jöhnk, K.D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P.M., and Stroom, J.M. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biol.* **14**: 495–512. doi:10.1111/j.1365-2486.2007.01510.x.

Kä, S., Mendoza-Vera, J.M., Bouvy, M., Champalbert, G., N’Gom-Kä, R., and Pagano, M. 2012. Can tropical freshwater zooplankton graze efficiently on cyanobacteria? *Hydrobiologia*, **679**: 119–138. doi:10.1007/s10750-011-0860-8.

Kankaanpää, H.T., Sipilä, V.O., Kuparinen, J.S., Ott, J.L., and Carmichael, W.W. 2001. Nodularin analyses and toxicity of a *Nodularia spumigena* (Nostocales, Cyanobacteria) water-bloom in the western Gulf of Finland, Baltic Sea, in August 1999. *Phycologia*, **40**: 268–274. doi:10.2216/i0031-8884-40-3-268.1.

Kearney, M.R., Matzelle, A., and Helmuth, B. 2012. Biomechanics meets the ecological niche: the importance of temporal data resolution. *J. Exp. Biol.* **215**: 922–933. doi:10.1242/jeb.059634. PMID:22357586.

Kokociński, M., Dziga, D., Spoo, L., Stefaniak, K., Jurczak, T., Mankiewicz-Boczek, J., and Meriluoto, J. 2009. First report of the cyanobacterial toxin cylindrospermopsin in the shallow, eutrophic lakes of western Poland. *Chemosphere*, **74**: 669–675. doi:10.1016/j.chemosphere.2008.10.027. PMID:19084257.

Kokociński, M., Stefaniak, K., Mankiewicz-Boczek, J., Izidorczyk, K., and Soininen, J. 2010. The ecology of the invasive cyanobacterium *Cylindrospermopsis raciborskii* (Nostocales, Cyanophyta) in two hypereutrophic lakes dominated by *Planktothrix agardhii* (Oscillatoriales, Cyanophyta). *Euro. J. Phycol.* **45**: 365–374. doi:10.1080/09670262.2010.492916.

Lagos, N., Onodera, H., Zagatto, P.A., Andrinolo, D., Azevedo, S.M.F.Q., and Oshima, Y. 1999. The first evidence of paralytic shellfish toxins in the freshwater cyanobacterium *Cylindrospermopsis raciborskii*, isolated from Brazil. *Toxicon*, **37**: 1359–1373. doi:10.1016/S0041-0101(99)00080-X. PMID:10414862.

Laugen, A.T., Hollander, J., Obst, M., and Strand, Å. 2015. The Pacific Oyster (*Crassostrea gigas*) invasion in Scandinavian coastal waters in a changing climate: impact on local ecosystem services. In *Biological invasions in aquatic and terrestrial systems: biogeography, ecological impacts, predictions and management*. Edited by J. Canning-Claude. Versita. In press.

Leflaive, J., and Ten-Hage, L. 2007. Algal and cyanobacterial secondary metabolites in freshwaters: a comparison of allelopathic compounds and toxins. *Freshwater Biol.* **52**: 199–214. doi:10.1111/j.1365-2427.2006.01689.x.

Legrand, C., Rengefors, K., Fistarol, G.O., and Granéli, E. 2003. Allelopathy in phytoplankton – biochemical, ecological, and evolutionary aspects. *Phycologia*, **42**: 406–419. doi:10.2216/i0031-8884-42-4-406.1.

Leonard, J.A., and Paerl, H.W. 2005. Zooplankton community structure, microzooplankton grazing impact, and seston energy content in the St. Johns River system, Florida as influenced by the toxic cyanobacterium *Cylindrospermopsis raciborskii*. *Hydrobiologia*, **537**: 89–97. doi:10.1007/s10750-004-2483-9.

- Lima, F.P., Ribeiro, P.A., Queiroz, N., Xavier, R., Tarroso, P., Hawkins, S.J., and Santos, A.M. 2007. Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Global Change Biol.* **13**: 2065–2077. doi:10.1111/j.1365-2486.2007.01424.x.
- Lürling, M., Eshetu, F., Faassen, E.J., Kosten, S., and Huszar, V.L.M. 2013. Comparison of cyanobacterial and green algal growth rates at different temperatures. *Freshwater Biol.* **58**: 552–559. doi:10.1111/j.1365-2427.2012.02866.x.
- McKnight, D.M., Howes, B.L., Taylor, C.D., and Goehring, D.D. 2000. Phytoplankton dynamics in a stably stratified Antarctic lake during winter darkness. *J. Phycol.* **36**: 852–861. doi:10.1046/j.1529-8817.2000.00031.x.
- Mehner, G., Leunert, F., Cirés, S., Jöhnk, K.D., Rucker, J., Nixdorf, B., and Wiedner, C. 2010. Competitiveness of invasive and native cyanobacteria from temperate freshwaters under various light and temperature conditions. *J. Plankton Res.* **32**: 1009–1021. doi:10.1093/plankt/fbq033.
- Meier, M., Andersson, H.C., Arheimer, B., Blenckner, T., Chubarenko, B., Donnelly, C., et al. 2012. Comparing reconstructed past variations and future projections of the Baltic Sea ecosystem — first results from multi-model ensemble simulations. *Environ. Res. Lett.* **7**: 034005. doi:10.1088/1748-9326/7/3/034005.
- Mello, M.M., Soares, M.C.S., Roland, F., and Lürling, M. 2012. Growth inhibition and colony formation in the cyanobacterium *Microcystis aeruginosa* induced by the cyanobacterium *Cylindrospermopsis raciborskii*. *J. Plankton Res.* **34**: 987–994. doi:10.1093/plankt/fbs056.
- Messineo, V., Melchiorre, S., Di Corcia, A., Gallo, P., and Bruno, M. 2010. Seasonal succession of *Cylindrospermopsis raciborskii* and *Aphanizomenon ovalisporum* blooms with cylindrospermopsin occurrence in the volcanic Lake Albano, central Italy. *Environ. Toxicol.* **25**: 18–27. doi:10.1002/tox.20469. PMID:19161233.
- Moisander, P.H., McClinton, E., and Paerl, H.W. 2002. Salinity effects on growth, photosynthetic parameters, and nitrogenase activity in estuarine planktonic cyanobacteria. *Microb. Ecol.* **43**: 432–442. doi:10.1007/s00248-001-1044-2. PMID:12043002.
- Moisander, P.H., Paerl, H.W., and Zehr, J.P. 2008. Effects of inorganic nitrogen on taxa-specific cyanobacterial growth and *nifH* expression in a subtropical estuary. *Limnol. Oceanogr.* **53**: 2519–2532. doi:10.4319/lo.2008.53.6.2519.
- Moisander, P.H., Cheshire, L.A., Braddy, J., Calandrino, E.S., Hoffman, M., Piehler, M.F., and Paerl, H.W. 2012. Facultative diazotrophy increases *Cylindrospermopsis raciborskii* competitiveness under fluctuating nitrogen availability. *FEMS Microbiol. Ecol.* **79**: 800–811. doi:10.1111/j.1574-6941.2011.01264.x. PMID:22126519.
- Moustaka-Gouni, M., Vardaka, E., Michaloudi, E., Kormas, K.A., Tryfon, E., Mihalatou, et al. 2006. Plankton food web structure in a eutrophic polymictic lake with a history in toxic cyanobacterial blooms. *Limnol. Oceanogr.* **51**: 715–727. doi:10.4319/lo.2006.51.1_part_2.0715.
- Mur, L.R., Skulberg, O.M., and Utكيلen, H. 1999. Cyanobacteria in the environment. In *Toxic cyanobacteria in water – a guide to public health consequences, monitoring and management*. Edited by I. Chorus and J. Bartram. E & FN Spon, WHO, London, England. pp. 15–40.
- Neilan, B.A., Saker, M.L., Fastner, J., Törökne, A., and Burns, B.P. 2003. Phylogeography of the invasive cyanobacterium *Cylindrospermopsis raciborskii*. *Mol. Ecol.* **12**: 133–140. doi:10.1046/j.1365-294X.2003.01709.x. PMID:12492883.
- Neumann, T. 2010. Climate-change effects on the Baltic Sea ecosystem: a model study. *J. Marine Syst.* **81**: 213–224. doi:10.1016/j.jmarsys.2009.12.001.
- Neumann, T., Eilola, K., Gustafsson, B., Müller-Karulis, B., Kuznetsov, I., Meier, H.E.M., and Savchuk, O.P. 2012. Extremes of temperature, oxygen and blooms in the Baltic Sea in a changing climate. *AMBIO*, **41**: 574–585. doi:10.1007/s13280-012-0321-2. PMID:22926880.
- Ohtani, I., Moore, R.E., and Runnegar, M.T.C. 1992. Cylindrospermopsin: a potent hepatotoxin from the blue-green alga *Cylindrospermopsis raciborskii*. *J. Am. Chem. Soc.* **114**: 7941–7942. doi:10.1021/ja00046a067.
- Omstedt, A., Edman, M., Anderson, L.G., and Laudon, H. 2010. Factors influencing the acid-base (pH) balance in the Baltic Sea: a sensitivity analysis. *Tellus*, **62B**: 280–295. doi:10.1111/j.1600-0889.2010.00463.x.
- O’Neil, J.M., Davis, T.W., Burford, M.A., and Gobler, C.J. 2012. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. *Harmful Algae*, **14**: 313–334. doi:10.1016/j.hal.2011.10.027.
- Padisák, J. 1997. *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Arch. Hydrobiol. Suppl. Monogr. Beit.* **107**: 563–593.
- Padisák, J., and Reynolds, C.S. 1998. Selection of phytoplankton associations in Lake Balaton, Hungary, in response to eutrophication and restoration measures, with special reference to cyanoprokaryotes. *Hydrobiologia*, **384**: 41–53. doi:10.1023/A:1003255529403.
- Paerl, H.W., and Huisman, J. 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ. Microbiol. Rep.* **1**: 27–37. doi:10.1111/j.1758-2229.2008.00004.x. PMID:23765717.
- Paerl, H.W., and Otten, T.G. 2013. Harmful cyanobacterial blooms: causes, consequences, and controls. *Microb. Ecol.* **65**: 995–1010. doi:10.1007/s00248-012-0159-y. PMID:23314096.
- Paerl, H.W., and Scott, J.T. 2010. Throwing fuel on the fire: synergistic effects of excessive nitrogen inputs and global warming on harmful algal blooms. *Environ. Sci. Technol.* **44**: 7756–7758. doi:10.1021/es102665e. PMID:20804137.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.
- Paulson, D.R. 2001. Recent odonata records from southern Florida — effects of global warming? *Int. J. Odonatol.* **4**: 57–69. doi:10.1080/13887890.2001.9748159.
- Piccini, C., Aubriot, L., Fabre, A., Amaral, V., González-Piana, M., Giani, A., et al. 2011. Genetic and eco-physiological differences of South American *Cylindrospermopsis raciborskii* isolates support the hypothesis of multiple ecotypes. *Harmful Algae*, **10**: 644–653. doi:10.1016/j.hal.2011.04.016.
- Pitkänen, H., Tamminen, T., Kangas, P., Huttula, T., Kivi, K., Kuosa, H., et al. 1993. Late summer trophic conditions in the north-east Gulf of Finland and the River Neva Estuary, Baltic Sea. *Estuarine, Coastal Shelf Sci.* **37**: 453–474. doi:10.1006/ecss.1993.1067.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change*, **3**: 919–925. doi:10.1038/nclimate1958.
- Posselt, A.J., Burford, M.A., and Shaw, G. 2009. Pulses of phosphate promote dominance of the toxic cyanophyte *Cylindrospermopsis raciborskii* in a subtropical water reservoir. *J. Phycol.* **45**: 540–546. doi:10.1111/j.1529-8817.2009.00675.x.
- Raateoja, M., Seppälä, J., and Kuosa, H. 2004. Bio-optical modelling of primary production in the SW Finnish coastal zone, Baltic Sea: fast repetition rate fluorometry in Case 2 waters. *Mar. Ecol. Prog. Ser.* **267**: 9–26. doi:10.3354/meps267009.
- Raudsepp, U. 2001. Interannual and seasonal temperature and salinity variations in the Gulf of Riga and corresponding saline water inflow from the Baltic Proper. *Nordic Hydrol.* **32**: 135–160. doi:10/2166/nh.2001.009.
- Reichwaldt, E.S., and Ghadouani, A. 2012. Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: between simplistic scenarios and complex dynamics. *Water Res.* **46**: 1372–1393. doi:10.1016/j.watres.2011.11.052. PMID:22169160.
- Reinikainen, M., Lindvall, F., Meriluoto, J.A.O., Repka, S., Sivonen, K., Spoof, L., and Wahlsten, M. 2002. Effects of dissolved cyanobacterial toxins on the survival and egg hatching of estuarine calanoid copepods. *Marine Biol.* **140**: 577–583. doi:10.1007/s00227-001-0720-6.
- Rzyski, P., Poniedziałek, B., Kokociński, M., Jurczak, T., Lipski, D., and Wiktorowicz, K. 2014. Interspecific allelopathy in cyanobacteria: *Cylindrospermopsis* and *Cylindrospermopsis raciborskii* effect on the growth and metabolism of *Microcystis aeruginosa*. *Harmful Algae*, **35**: 1–8. doi:10.1016/j.hal.2014.03.002.
- Saker, M.L., and Griffiths, D.J. 2000. The effect of temperature on growth and cylindrospermopsin content of seven isolates of *Cylindrospermopsis raciborskii* (Nostocales, Cyanophyceae) from water bodies in northern Australia. *Phycologia*, **39**: 349–354. doi:10.2216/i0031-8884-39-4-349-1.
- Saker, M.L., Nogueira, I.C.G., and Vasconcelos, V.M. 2003. Distribution and toxicity of *Cylindrospermopsis raciborskii* (cyanobacteria) in Portuguese freshwaters. *Limneta*, **22**: 129–136.
- Shapiro, J. 1973. Blue-green algae: why they become dominant. *Science*, **179**: 382–384. doi:10.1126/science.179.4071.382. PMID:4630211.
- Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? *Biol. Invasions*, **13**: 1255–1268. doi:10.1007/s10530-011-9956-3.
- Sinha, R., Pearson, L.A., Davis, T.W., Burford, M.A., Orr, P.T., and Neilan, B.A. 2012. Increased incidence of *Cylindrospermopsis raciborskii* in temperate zones — is climate change responsible? *Water Res.* **46**: 1408–1419. doi:10.1016/j.watres.2011.12.019. PMID:22284981.
- Sivonen, K., Halinen, K., Sihvonen, L.M., Koskeniemi, K., Sinkko, H., Rantasarikka, K., Moisander, P.H., and Lyra, C. 2007. Bacterial diversity and function in the Baltic Sea with an emphasis on cyanobacteria. *AMBIO*, **36**: 180–185. doi:10.1579/0044-7447(2007)36%5B180:BDAFIT%5D2.0.CO;2. PMID:17520932.
- Smith, D.J., Griffin, D.W., and Jaffe, D.A. 2011. The high life: transport of microbes in the atmosphere. *Eos Trans. Am. Geophys. Union*, **92**: 249–250. doi:10.1029/2011EO300001.
- Stal, L.J., Albertano, P., Bergman, B., von Bröckel, K., Gallone, J.R., Hayes, P.K., et al. 2003. BASIC: Baltic Sea cyanobacteria. An investigation of the structure and dynamics of water blooms of cyanobacteria in the Baltic Sea — responses to a changing environment. *Cont. Shelf Res.* **23**: 1695–1714. doi:10.1016/j.csr.2003.06.001.
- Stewart, I., Eaglesham, G.K., McGregor, G.B., Chong, R., Seawright, A.A., Wickramasinghe, W.A., et al. 2012. First report of a toxic *Nodularia spumigena* (Nostocales/Cyanobacteria) bloom in sub-tropical Australia. II. Bioaccumulation of nodularin in isolated populations of mullet (Mugilidae). *Int. J. Environ. Res. Public Health*, **9**: 2412–2443. doi:10.3390/ijerph9072412.
- Suikkanen, S., Laamanen, M., and Huttunen, M. 2007. Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. *Estuarine, Coastal Shelf Sci.* **71**: 580–592. doi:10.1016/j.ecss.2006.09.004.
- Suikkanen, S., Kaartokallio, H., Hällfors, S., Huttunen, M., and Laamanen, M. 2010. Life cycle strategies of bloom-forming, filamentous cyanobacteria in the Baltic Sea. *Deep-Sea Res. II*, **57**: 199–209. doi:10.1016/j.dsr2.2009.09.014.
- Suikkanen, S., Pulina, S., Engström-Öst, J., Lehtiniemi, M., Lehtinen, S., and Brutemark, A. 2013. Climate change and eutrophication induced shifts in

- northern summer plankton communities. *PLoS One*, **8**: e66475. doi:10.1371/journal.pone.0066475. PMID:23776676.
- Sukenik, A., Hadas, O., Kaplan, A., and Quesada, A. 2012. Invasion of Nostocales (Cyanobacteria) to subtropical and temperate freshwater lakes — physiological, regional, and global driving forces. *Front. Microbiol.* **3**: 1–9. doi:10.3389/fmicb.2012.00086. PMID:22408640.
- Taranu, Z.E., Zurawell, R.W., Pick, F., and Gregory-Eaves, I. 2012. Predicting cyanobacterial dynamics in the face of global change: the importance of scale and environmental context. *Global Change Biol.* **18**: 3477–3490. doi:10.1111/gcb.12015.
- Theoharides, K.A., and Dukes, J.S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* **176**: 256–273. doi:10.1111/j.1469-8137.2007.02207.x. PMID:17822399.
- Vilá, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* **14**: 702–708. doi:10.1111/j.1461-0248.2011.01628.x. PMID:21592274.
- Wiedner, C., Rucker, J., Brüggemann, R., and Nixdorf, B. 2007. Climate change affects timing and size of populations of an invasive cyanobacterium in temperate regions. *Oecologia*, **152**: 473–484. doi:10.1007/s00442-007-0683-5. PMID:17375336.
- Wu, Z., Shi, J., and Li, R. 2009. Comparative studies on photosynthesis and phosphate metabolism of *Cylindrospermopsis raciborskii* with *Microcystis aeruginosa* and *Aphanizomenon flos-aquae*. *Harmful Algae*, **8**: 910–915. doi:10.1016/j.hal.2009.05.002.
- Zagatto, P.A., Buratini, S.V., Aragão, M.A., and Ferrão-Filho, A.S. 2012. Neurotoxicity of two *Cylindrospermopsis raciborskii* (cyanobacteria) strains to mice, *Daphnia*, and fish. *Environ. Toxicol. Chem.* **31**: 857–862. doi:10.1002/etc.1759. PMID:22278803.