Projections of effects of climate change on the spatial distribution of two harmful algal genera in three regions of the globe: a coupled oceanographic-biogeochemical model analysis

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Abstract

Harmful algal blooms (HABs), those proliferations of algae that can cause fish kills, contaminate seafood with toxins, form unsightly scums, or detrimentally alter ecosystem function have been increasing in frequency, magnitude, and duration worldwide. Here, using a global modeling approach, we show, for three regionsof the globe, the potential effects of nutrient loading and climate change for two HAB genera, pelagic *Prorocentrum* and *Karenia*, each with differing physiological characteristics for growth. The projections (end of century, 2090-2100) are based on climate change resulting from the A1B scenario of the Intergovernmental Panel on Climate Change Institut Pierre Simon Laplace Climate Model (IPCC, IPSL-CM4), applied in a coupled oceanographic-biogeochemical model, combined with a suite of assumed physiological "rules" for genera-specific bloom development. Based on these models, an expansion in area and/or number of months annually conducive to development of these HABs along the NW European Shelf-Baltic Sea system and NE Asia was projected for both HAB genera, but no expansion (*Prorocentrum* spp.), or actual contraction in area and months conducive for blooms (*Karenia* spp.), was projected in the SE Asian domain. The implications of these projections, especially for Northern Europe, are shifts in vulnerability of coastal systems to HAB events, increased regional HAB impacts to aquaculture, increased risks to human health and ecosystems, and economic consequences of these events due to losses to fisheries and ecosystem services.

Introduction

Harmful algal blooms (HABs), those proliferations of algae that can cause fish kills, contaminate seafood with toxins, form unsightly scums, or detrimentally alter ecosystem function have been increasing in frequency, magnitude, and duration worldwide, largely as a function of eutrophication and introduction of foreign species, as well as changing environmental conditions due to climate (Anderson *et al.*, 2002; Heisler *et al.,* 2008; Edwards *et al.,* 2006; Fu *et al.,* 2012). Climate change is projected to have substantial effects on the frequency and abundance of HABs because of the complexity of factors that may change as climate changes and their combined effects on the growth or habitat of HABs (Fu *et al,*. 2012). Examples of factors, in addition to temperature, affecting HABs that may change due to greenhouse warming include altered salinity due to increased precipitation and runoff, increased stratification, and changes in nutrient and light regimes (*e.g.,* Boyd & Doney, 2003; Hutchins *et al.,* 2009; Fu *et al.,* 2012). In addition, nutrient loads are likely to continue to increase in the coming years due to increased population, increased fossil fuel burning (and associated discharge of NO_x), increased fertilizer use and development of concentrated animal operations, including aquaculture operations that have little to no waste treatment (*e.g.,* Burkholder *et al.,* 2007; Glibert *et al.,* 2010; Bouwman *et al.,* 2011, 2013). Nutrient trends are expected to result in not only increased total nutrient loads but also changes in nutrient proportions, including increased proportions of reduced relative to oxidized forms of nitrogen and increased nitrogen:phosphorus (N:P) ratios. The former is a result of increased anthropogenic use of reduced chemical fertilizers like urea, and waste release from animal operations, including aquaculture. The latter is a result of increased anthropogenic use of N relative to P (Peñuelas *et al.,* 2012; Glibert *et al,*. 2013).

Here, we have developed a suite of model projections of the effect of climate change on HAB distribution in several regions of the globe, NW European Shelf-Baltic Sea system, NE Asia, and SE Asia. The projections (end of century, 2090-2100) are based on climate change resulting from the A1B scenario of the Intergovernmental Panel on Climate Change Institut Pierre Simon Laplace Climate Model (IPCC, IPSL-CM4; Marti *et al.,* 2004), applied in a coupled oceanographic-biogeochemical model (Holt *et al.,* 2009), combined with a suite of assumed physiological "rules" for genera-specific bloom development. The outputs of these simulations have previously been used to explore the impacts of climate change on fisheries (Blanchard *et al.,* 2012), the bio-economics of fishmeal including the consequences for aquaculture (Merino *et al,.* 2012) and an assessment of the impacts of climate change on marine ecosystemproduction in societies dependent on fisheries (Barange *et al.,* 2014).

Recognizing that there is a wide diversity of species that comprise HABs and that the conditions conducive to their development vary considerably, we have focused here only on two pelagic dinoflagellate species groups that have global distribution, significant ecological or human health effects, and about which much has been characterized with respect to their physiology: *Prorocentrum* spp. and *Karenia* spp. (Chang, 1996; Heil *et al.,* 2005; Vargo *et al.,* 2008; Glibert *et al.,* 2008, 2012; Brand *et al.,* 2012). Planktonic *Prorocentrum* species are among the most commonly recognized harmful algae that are increasing in frequency, duration, and magnitude globally (Heil *et al*., 2005; Glibert *et al*., 2008); as of 2003, at least 56 species within the genus *Prorocentrum* were known from estuarine and marine waters (Gómez, 2005) and of these, at least six species have been shown to form high biomass blooms (Glibert et al., 2012 and references therein). The global expansion of the best-studied pelagic *Prorocentrum* species, *P. minimum*, suggests that this species is spreading in concert with eutrophication (Heil *et a*l., 2005; Glibert *et al.,* 2008). *Karenia* spp. is also globally distributed, with the most common planktonic species being *K. mikimotoi* and *K. brevis*. However, there has been much confusion in the literature regarding this genera and closely related genera, and older reports either refer to these species as *Gymnodinium mikimotoi*, *Gymnodinium breve* or *Gyrodinium aureolum* (Chang, 1996). In terms of many physiological and growth strategies related to nutrient acquisition, a related genera to *Karenia* is *Karlodinium* (formerly recorded as *Gyrodinium galatheanum, Gymnodinium galatheanum* and *Karlodiniummicrum;* Adolf *et al.,* 2006; Deeds, 2009; Li *et al.*, 2010). This genera is also a widespread dinoflagellate which has caused HABs in coastal waters of Southwest Africa, Europe, United States, and Western Australia (Li *et al*., 2000; Zhang *et al*., 2008; Deeds, 2009).

Prorocentrum spp. and *Karenia* spp. have been shown to have distinct habitat preferences and different adaptive strategies with respect to both nutrients and to turbulence (Smayda & Reynolds, 2001; Li *et al*., 2009, 2010). *Prorocentrum* spp. are generally small cells (average length 15~22 μm, width 9~14 μm) and are typically rapidly growing bloom-formers in nutrient rich, near-shore regions. Conversely,*Karenia* spp. are generally larger cells (average length 18-37 µm, width 14-35 µm) and are relatively slower growing, and are generally considered to be off-shore species (Smayda & Reynolds, 2001). The ambient N:P ratio has been suggested to be an important nutrient parameter regulating the *Prorocentrum* and *Karenia* spp. bloom progression (Li *et al.,* 2009; Li *et al*., 2010). These contrasting genera also represent HABs with distinct ecosystem impacts; pelagic *Prorocentrum* spp. blooms tend to be high-biomass and disruptive to food webs (*e.g.,* Heil *et al.* 2005; Glibert *et al.* 2008, 2012), whereas those of *Karenia* spp., may be high-biomass, but more typically are toxic with impacts for both human and wildlife heath (Landsberg, 2002; Backer & McGillicuddy, 2006; Vargo *et al.,* 2012; Brand *et al.,* 2012).

Similarly, among the many regions of the world wherein these HAB genera are found, we have focused on several highly contrasting regions. These regions all have intensive aquaculture, but varying anthropogenic nutrient loading. Among the regions, Asia (both NE and SE Asia) has experienced significant increases in nutrient inputs – and HAB outbreaks - over the past several decades of rapid agricultural and industrial development (Sidharta, 2005; Chai *et al*., 2006; Li *et al.,* 2009). These HAB genera and regions thus present interesting contrasts.

Methods

Model Description

The model system used in this work is the Global Coastal Ocean Modelling System (GCOMS; Holt *et al.* 2009). GCOMS is derived from the oceanographic model POLCOMS (Holt & James, 2001) coupled to the biogeochemical model ERSEM (Blackford et al., 2004; Fig. 1). POLCOMS is a 3D baroclinic circulation model, with adetailed description of shelf seas transport processes. ERSEM is a state-of-the-art biogeochemical with 4 plankton functional types for phytoplankton (picoplankton, flagellates, diatoms, and dinoflagellates), 3 for zooplankton (microzooplankton, mesozooplankton and hetertrophic dinoflagellates) and 1 for bacteria. The model parameterizes phytoplankton and bacteria with variable C:N:P stoichiometry, so the model is able to simulate acclimation of organisms to different nutrient regimes. The macronutrients N and P are included in different forms: dissolved inorganic, dissolved organic and particulate organic, and within the dissolved inorganic N forms, a differentiation is made between ammonium (NH_4^+) and nitrate (NO_3^-; Fig 1). Mineralisation of organic matter can occur either in the water column or in the benthos. The former is partly directly simulated by bacterial dynamics, and partly simulated with an implicit first order kinetics to include all process not directly mediated by bacteria. Benthic mineralisation of particulate organic nutrient is simulated with simple first order kinetics. Atmospheric deposition of nutrient is not considered.

In this work we have considered three domains, the NW European Shelf-Baltic Sea system, NE Asia, and SE Asia. These domains and their associated boundary conditions were defined using GCOMS (Holt *et al.,* 2009). All model domains have a horizontal resolution of 1/10º and 42 s-coordinates levels, with bathymetry derived from the GEBCO 1-arcminute dataset (GEBCO, 2013).

Two time slices were run using boundary conditions obtained from the Institut Pierre Simon Laplace Climate Model (IPSL-CM4; Marti *et al*., 2006), run for the 4th IPCC Assessment Report on Climate Change (Solomon *et al.,* 2007) for the period 1980-1990 for the "present day" scenario, and 2090-2100 under the IPCC-AR4 A1B scenario for the "future" scenario. Among the IPCC scenarios, the A1 storyline suggests a period of rapid economic growth and population growth by mid-century, followed by a slowing due to rapid technological development, and more efficient technologies (Nakićenović et al., 2000). Within the A1 scenario family, the A1B assumptions include a balance of energy sources and new technologies, and the range of emission projections is among the mid-line estimates of IPCC model ensembles. For each time slice, a total of 13 years of simulations were run, with the final 10 used to capture both the signal as well as natural variability; each time slice is the mean of these 10 years. A third set of 're-analysis' simulations (not shown) was also performed, providing a benchmark against which the subsequent IPSL-CM4 forced simulations could be assessed. This was not a prerequisite to gauge the fidelity of model results in the IPSL-CM4 forced scenarios, but toprovide a degree of confidence in the model code in the context of the present day.

The boundary condition data provided to the regional simulations consisted of wind stress, cloud cover, mean sea level pressure, air temperature, downwelling shortwave and longwave radiation, and freshwater fluxes from the atmospheric component of the IPSL-CM4 (Fig. 1). From the ocean component of IPSL-CM4, temperature, salinity, sea surface elevation and zonal and meridional velocities were required.

Riverine inputs to ERSEM were parameterized using output from the Global Nutrient Export from WaterSheds (NEWS) model (Seitzinger *et al.,* 2005). Global NEWS is a modeled database of riverine nutrient loads by form and major source (Seitzinger *et al.,* 2005). The Global NEWS models are based on data from over 5000 exoreic basins worldwide at a resolution of 0.5° x 0.5°. In estimating nutrient flux at river mouths, the NEWS models take into account both natural sources such as N_2 fixation and P weathering and anthropogenic sources, including non-point inputs from fertilizer (by crop type), N_2 fixation by crops, atmospheric N deposition, and manure (by animal species) and point sources from sewage, as estimated by human population and treatment level (Seitzinger *et al.,* 2005). The models also account for in-river hydrological and physical factors, including water runoff, precipitation intensity, land use and slope, as well as in-water removal processes such as dams and reservoirs and consumptive water use. The Global NEWS models have previously been validated with a separate data set not used in model formulation, as described by Dumont *et al.* (2005) and Harrison *et al.* (2005).

To avoid any blurring of attribution between climate change and projected changes in anthropogenic nutrient loading, nutrient loads per se were not changed in the future projections even though it is expected that anthropogenic nutrient loading will continue and future loads may have altered nutrient stoichiometry.

HAB Parameterization

Based on literature reviews (Table 1; Heil *et al.,* 2005; Vargo *et al.,* 2008; Glibert *et al.*, 2012; Brand *et al.,* 2012), a suite of physical and chemical (nutrient) parameters previously associated with positive growth of the selected HAB genera were defined. The physical habitat was defined based on a temperature and salinity envelope that supports growth. As our goal was to define potential habitat rather than growth rates, it was not necessary to parameterize individual rates as a function of each parameter for each HAB genera.

To define the chemical habitat for growth or propensity for toxicity, two nutrient ratios were used. The first is the ratio of water-column NH_4^+:NO_3^- concentrations; it is assumed that when the redox state of the nutrient environment shifts to proportionately more reduced forms of N, HAB species will be favoured (*e.g.,* Glibert *et al.,* 2006; Heil *et al.,* 2008; Heisler *et al.,* 2008; Li *et al.,* 2009). The second nutrient ratio is the inorganic N:P ratio, and it has been used to assess the potential toxicity of the HABs: it has been shown previously that many HAB species are proportionately more toxic when nutrient availability is not in classic stoichiometric proportion, typically defined by the Redfield ratio of 16:1 on a molar basis (Granéli & Flynn, 2006; Glibert & Burkholder, 2011; Sun *et al*., 2011; Fu *et al.,* 2012; Hardison *et al.,* 2013). Many HAB species have been shown to increase cellular toxin content by many-fold when growth becomes nutrient, especially P limited (e.g., Graneli & Flynn, 2006), and *Karenia* spp. is among those displaying this trend (Hardison *et al.,* 2013). Toxicity of some *Prorocentrum* species remains controversial (Heil *et al.,* 2005) and among the six harmful *Prorocentrum* species that are predominantly planktonic, thus far only *P. minimum* has been described as potentially toxic (Glibert *et al.,* 2012). While we have defined the physical and nutrient habitat based on literature reviews of these HAB genera, it must be borne in mind that we are using these species types as representative model HAB types.

Model Projections

The defined physical and nutrient criteria were applied to the GCOMS model of the coasts of NW Europe, NE and SE Asia (Holt *et al.* 2009). The model output defined the spatially-explicit fraction of time during the year when conditions met the individually defined criteria and the fraction of time when all criteria were collectively met. Importantly, the model output does not define the potential strength of a bloom (*i.e.,* chlorophyll or cell biomass), only the potential suitability of the habitat and the duration over which such suitability may occur.

Monthly 2D outputs from the regional simulations of sea surface temperature and salinity (SST, SSS), and of average nutrient concentration by form in the mixed layer depth were analyzed. These rules were applied in every single grid point of the 2D outputs each month to verify if the model was predicting favourable conditions for a bloom or not.

Results

Model Skill

The model skill for simulating seasonal to annual SST and SSS and chlorophyll at the domain scale is summarised by a Taylor diagram (Taylor, 2001; Fig. 2). The time- mean and spatial- mean components were removed and each model value normalised by the observational standard deviation. The model demonstrates skill in reproducing all three variables; the skill is best in the SST. It is important to emphasize that for the model projections herein, chlorophyll accumulations are not illustrated; rather, we are illustrating the time and space over which suitable habitat conditions might exist for such accumulations to occur. The Taylor diagram also shows that on seasonal to annual timescales the skill is similar between the re-analysis-forced and IPSL-CM4 present-day-forced regional simulations. However, biases exist in the mean values of these variables as there is reduced skill in the IPSL-CM4 simulation resolving the mean state of the physical system and of POLCOMS-ERSEM to capture mean state of the ecosystem (Table 2).

Model Projections

The model output shows the potential for the effects of nutrient loading and climate change in terms of projected change in area and/or fraction of time annually conducive to HABs. The projections suggest variable habitat expansion of HABs under the applied assumptions of climate change (Fig. 3-5). Along the Northern European coast, a considerableexpansion in the number of months annually conducive to both types of HAB species is projected, but conditions conducive to expansion of *Prorocentrum*-type HAB species are projected to be greater than those of *Karenia*-type species (Fig. 3). In NE Asian waters, a lesser spatial expansion is projected, but an expansion nonetheless (Fig. 4). While conditions suitable for *Prorocentrum* are projected to lead to greater geographic extent of the blooms, also projected is a reduction in the time period supportive of these blooms in the regions where they now occur. Interestingly, for the SE Asian domain, the projection for the future spatial extent of *Prorocentrum*-type HABs is little changed compared to the present, but for the *Karenia*-type HABs it suggests contraction (Fig. 5). Thus, fewer outbreaks of *Karenia*-type blooms would be expected under the future modeled conditions. The primary reason for this, in the model, is assumed to be exceedance of the temperature range suitable for growth.

For conditions herein defined as supportive of increased toxicity (i.e., imbalanced N:P ratios), the overall spatial trends by region and species are similar (not shown), but, as illustrated for *Karenia* spp. in Northern Europe (future condition) and in NE Asian waters (present condition), the months conducive to a toxic condition are not directly related to the number of months conducive to species presence (Fig. 6). Only a percentage of the periods that support growth also support potentially toxic conditions.

In order to assess the significance of each driver (temperature, salinity, changes in nutrient ratios) in terms of how they affect the potential habitat suitability for both genera in both the present condition as well as the future, each variable was applied separately for each time period. The variables were then combined in all possible combinations to derive 8 different conditions for each HAB and each regional domain. The total number of occurrences when all three conditions were met per model run (monthly resolution) was determined and then normalized by the total number of pixels of the domain in the entire 120 months period (10 years each present and future time slices; Table 3). For the NW

European/Baltic Sea, temperature was by far the more important driver for both species; when salinity and nutrients were held at present day values and temperature set to future conditions, *Prorocentrum* spp. was estimated to increase ~300%, but *Karenia* spp. was estimated to increase far more, >2700% (Table 3). When present conditions were held for temperature and nutrients, but salinity allowed to change with future condition, both genera were estimated to increase ~100%. When two or more factors were changes to the A1B conditions, Prorocetnrum spp. increased ~700-800% and Karenia increased ~2000-4000% in the Northern European/Baltic Sea domain. However, holding salinity and temperate at present day values and changing nutrients to the future state condition actually resulted in a decrease of both genera. Changing temperature, either alone or in combination with the other factors was related to a ~60-115% change in *Karenia* spp. in NE Asia, but the same was not observed for *Prorocentrum.* In SE Asia, all factors (except salinity) individually and in combination were associated with declines in both species groups. The greater influence of temperature in this analysis is not surprising as it was the factor that was manipulated by design in the future state analysis. The salinity and nutrient factors changed in the future state analysis only as a result of biogeochemical changes, not anthropogenic changes.

Discussion

Model Fidelity with Current Conditions

The outcome of the model projections for current conditions was compared with literature reports of blooms of these species groups for these regions where available. The most robust data set for comparison is from the time series of *Prorocentrum* spp. in the NW European/Baltic Sea coast reported by Edwards *et al.* (2006) although numerous additional reports of such blooms are available for the region (e.g., Hajdu *et al.,* 2000, 2005; Olenina *et al.,* 2010); the model projection for this region revealed remarkable fidelity with these reports

(Fig. 7). Note that the Edwards *et al.* (2006) analysis, although representing Prorocetnrum spp. distributions, the data include benthic as well as pelagic species. The Olenina et al. (2010) study is of *P. minimum.*

For the NE Asian coast, blooms of *Prorocentrum* spp. and *Karenia* spp. are now well documented and their expansion in recent decades represent some of the best documented examples of the relationship between HABs and eutrophication (Heisler *et al.,* 2008; Glibert *et al.,* 2008). These blooms are dominated by the planktonic species *P. donghaiense* (Lu & Goebel, 2001; Zhou *et al*., 2003, 2008; Lu *et al*., 2005; Lou *et al*., 2006; Wang & Wu, 2008; Furuya *et al.,* 2010). Massive blooms up to 10,000 km^2 in areal extent have occurred in late spring (Zhou *et al*., 2008; Li *et al*., 2009, 2010; Lu *et al*., 2011). Based on both false color images of the East China Sea acquired by MODIS Terra during a bloom in 2005 (Lou *et al.,* 2006) and a “red tide” bloom index developed from Seawifs data (Ahn & Shannmugan, 2006), good fidelity between the current conditions projected in the model and the region of intense red tide blooms was found (Fig. 8).

For the SE Asian coast, while there is comparatively less research available on these types of blooms there than on the other sites, it has nevertheless been well documented that massive “red tides” occur (e.g., Tang *et al.,* 2006). *Karenia* spp. has been shown to cause blooms that have resulted in fish kills in the South China Sea (Chen *et al*., 2011), and *K. brevis* (reported as *Gymnodinium breve*) has been reported to cause blooms in Jakarta Bay (Sidharta, 2005), while *Karlodinium veneficum* has been reported in Malaysian waters (Lim *et al*., 2012). Additionally, blooms of *P. minimum* have been recorded to have lasted for months off the coast of Malaysia (Lim *et al*., 2012) and *Prorocentrum* spp. (typically *P. micans*) is among the most common HAB dinoflagellates along the Indonesian coast (Thoha *et al.,* 2007).

Assumptions and Caveats

The aim of the approach was to develop a tool that could be applied, and further refined in future analyses, to project the potential change in these HAB types to climate, and the interaction between climate and nutrient biogeochemistry. Thus, the approach provided can be considered a demonstration of concept and can be amplified and fine-tuned with more or different parameters or mechanistic approaches as knowledge of these and other HAB genera and species advances. As with any model, the suite of parameters used here to define species habitat, is a simplification. Some of the assumptions, caveats, and potential for advancement are important to note. The assumptions used herein illustrate the applicability of the approach and can befurther refined as knowledge regarding physiology is change or altered to project the outcome of different species groups or in different regimes as needs develop.

Nutrient ratios rather than absolute nutrient loads were stressed in this model. There were several reasons for this. First, whereas nutrient loads and concentrations set the total production of an ecosystem, nutrient ratios can regulate the composition of the microbial community (Glibert & Burkholder, 2006; Heisler *et al.,* 2008 and references therein). Second, inasmuch as the goal was to identify the likelihood of conditions supportive of blooms, rather than their strength or magnitude, absolute concentrations were not necessary. A nutrient ratio approach allowed the interrogation of species types that did not necessarily constitute the bulk of primary production. By applying the model to the contrasting model HAB genera described above, the power of this approach was demonstrated for HABs that may form either high biomass blooms or toxic outbreaks that occur in relatively low concentration with a matrix of other phytoplankton within the assemblage.

Explicit anthropogenic increases in nutrient loading were not included in these scenarios. Nutrient loads are projected to increase in Asia and to stabilize in Europe over the next century (Seitzinger *et al.,* 2010). However, it is likely that N loads will continue to exceed those of P in Europe and possibly elsewhere with the projected P shortage anticipated in coming decades (Cordell *et al.,* 2009), leading to changes in the potential for toxic vs. nontoxic blooms. Moreover, particularly in Asia, nutrient loads may change in chemical form; the loading of chemically reduced N may increase due to increasing urea and NH_4^+-based fertilizer use and likely increases in atmospheric NH_4^+ deposition and aquaculture (Glibert *et al.,* 2006; Bouwman *et al.,* 2009, 2011, 2013). Expansion in coastal aquaculture may also increase both reduced relative to oxidized N forms and N:P ratios (Bureau & Hua, 2010; Bouwman *et al.,* 2011, 2013). As noted above, although anthropogenic nutrient changes are not included in the analysis herein, the parameterization of the model does account for changes in nutrient form and ratio that may develop over time due to changes in biogeochemistry due to the effects of seawater warming. Increases in nutrient load would be expected to accelerate these changes.

Another simplification of the model is that the physiological "rules" applied here do not account for all that is known about the nutritional diversity or habitat preference of many HABs. In particular, dissolved organic nutrients or particulate nutrients were not included as nutritional substrates but known to contribute substantially to some HABs (Heisler *et al.,* 2008; Burkholder *et al.,* 2008; Jeong *et al.,* 2010; Flynn *et al.,* 2013). Yet, even with the suite of relatively simple rules defining habitat, remarkable fidelity with current conditions spatially was achieved, at least for the N. European and NW Asiatic regions. There is much yet to be understood about how and why HAB dinoflagellates form and when and where they do. For model projections, the key is identifying which parameters may be most insightful for characterizing spatial and temporal distributions.

In terms of the physical model, it is important to underscore that the horizontal scales of the models applied do not fully resolve the coastal zone. Low resolution of the model near-shore may tend to yield underestimations of local, near coastal nutrient concentrations. Thus, these projections may underestimate the potential for HAB growth currently- or future expansion- in these immediate regions. The immediate coasts are - and will be - subject to considerably greater effects of climate change, due to disproportionate warming of shallow waters and different physics at the local scale. As coastal models become more fully resolved, such an approach can be expanded to resolve the effects at finer scales.

Finally, these projections are based on a mid-line, or conservative assumption of climate change. As climate models improve, as physical dynamics at the coastal zone become more fully incorporated into coupled physical-biogeochemical models, as more is learned about projected anthropogenic nutrient changes, and as more is learned regarding the physiological niches of HAB species, additional and more detailed scenarios can be developed, allowing resource managers to suitably plan for future conditions. In spite of these caveats, our projections show fidelity with current HAB distributions for the regions for which ground-truth data are available and suggest an expansion of HABs and impacts in these regions.

Physical-Chemical Parameter Match-Mismatch

The model output suggests that bloom expansion (or contraction) not only depends on the change in abiotic conditions supportive of their growth, but also on the temporal or spatial match of expansion of these parameters. In order for blooms to occur, all criteria for growth must be met at the same time and location. Any scenario that alters one set of matching parameters in time or space without altering the other criteria likely leads to a “mismatch” of conditions and a lesser likelihood for blooms to develop.

On individual bases, the projected increase in temperature and increase in nutrient conditions suggest an even greater potential for expansion of these blooms, but the overlap of these conditions limits the realization of these effects. For example, as illustrated for *Prorocentrum*-type physical and chemical niches in the NW European Shelf system (Fig. 9a,b), in both the present day and future scenario, salinity is seemingly suitable year-round for growth, but the optimal conditions in terms of temperature (months 7-10 at present, months 6-12 in the future scenario) and nutrients (months 5-7) are slightly displaced in time. Despite some temporal overlap, in the current scenario there is a significant spatial mismatch that limits the frequency of favoring blooming conditions (Fig. 9c). The expansion of the physical niche in the A1B scenario leads to a general increase in likelihood of conditions conducive to blooms (Fig. 9d). Climate warming not only directly affects rates of growth of these species, but also affects the environment indirectly through increased stratification, nutrient recycling and other changes in biogeochemistry (*e.g.,* Edwards *et al.,* 2006). Ultimately both physical and chemical niches must overlap temporally and spatially for blooms to develop.

The temporal mismatch in suitability of conditions for growth should not be viewed as evidence for limited potential for expansion. Rather, such a difference points to the possibility of expansion should there be a change in the timing of any one of the parameters. Climate forcing may alter the timing of nutrient loads relative to seasonal warming which may, in turn, alter the alignment of suitable conditions. Such a difference may occur, for example due to extreme weather events that may provide an injection of favorable nutrients later in the year. There is mounting evidence that climate variability and increased frequency of extreme weather events increase due to climate change (Solomon *et al.,* 2007).

Conclusions

This exercise has identified significant change in potential habitat suitability for two HAB types in different regions of the globe. Expansion of both HAB genera is projected in the NW European/Baltic Sea region and an expansion of *Karenia*-type blooms is projected in NE Asia. The implications of these projections are shifts in vulnerability of coastal systems to HAB events, increased regional HAB impacts to aquaculture, increased risks to human health and ecosystems, and economic consequences of these events due to losses to fisheries and ecosystem services (Hoagland & Scatasta, 2006). In regions where contraction of suitability for *Karenia*-type species to occur is projected, *i.e.,* SE Asia, it must be borne in mind that this projection is based on one set of physiological parameters and not all HAB types of major concern are represented (Sidharta, 2005; Lim *et al.,* 2012); it remains entirely possible that other species with greater temperature range could expand their ranges while *Karenia*-type events contract.

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References

Adolf JE, Stoecker DK, Harding LW (2006) The balance of autotrophy and heterotrophy during mixotrophic growth of *Karlodinium micrum* (Dinophyceae). *Journal of Plankton Research,* **28**, 737-751

Ahn Y-H, Shannmugam P (2006) Detecting the red tide algal blooms from satellite ocean color observations in optically complex Northeastern-Asia coastal waters. *Remote Sensing of the Environment,* **103**, 419-437.

Anderson DM, Glibert PM, Burkholder JM (2002) Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries,* **25**, 562-584.

Backer LC, McGillicuddy DJ Jr (2006) Harmful algal blooms at the interface between coastal oceanography and human health. *Oceanography*, **19**, 94- 106.

Barange M, Merino G, Blanchard J.L, Scholtens J, Harle J, Allison E.H, Allen J.I, Holt J. and Jennings S (2014) Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change*, doi: 10.1038/NCLIMATE2119

Blackford JC, Allen JI, Gilbert FJ (2004) Ecosystem dynamics at six contrasting sites: a generic modelling study. *Journal of Marine Systems* **52**, 191-215.

Blanchard JL, Jennings S, Holmes R *et al.* (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems *Philosophical Transactions of the Royal Society B: Biological Sciences,* **367**, 2979-2989.

Bouwman AF, Beusen AHW, Billen G (2009) Human alteration of the global nitrogen and phosphorus soil balances for the period 1970-2050. *Global Biogeochemical Cycles,* **23**, doi:10.1029/2009GB003576.

Bouwman AF, Beusen AHW, Overbeek CC *et al.* (2013) Hindcasts and future projects of global inland and coastal nitrogen and phosphorus loads due to finfish aquaculture. *Reviews in Fisheries Science,* **21**, 112-156.

Bouwman AF, Pawlowski M, Liu C *et al.* (2011) Global hindcasts and future projections of coastal nitrogen and phosphorus loads due to shellfish and seaweed aquaculture. *Reviews in Fisheries Sci*ence, **19**, 331-357.

Boyd PW, Doney SC (2003) The impact of climate change and feedback processes on the ocean carbon cycle. In: *Ocean biogeochemistry – the role of the ocean carbon cycle in global change* (ed Fasham MJR), pp. 157-193. Springer-Verlag. Berlin.

Brand LE, Campbell L, Bresnan E (2012) *Karenia*: The biology and ecology of a toxic genus. *Harmful Algae,* **14**, 156-178.

Bureau DP, Hua K (2010) Towards effective nutritional management of waste outputs in aquaculture, with particular reference to salmonid aquaculture operations. *Aquaculture Research,* **41**, 777-792.

Burkholder JM, Glibert PM, Skelton H (2008) Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae,* **8**, 77-93.

Burkholder JM, Libra B, Weyer P *et al.* (2007) Impacts of waste from concentrated animal feeding operations on water quality. *Environmental Health Perspectives 115*, 308-312.

Chai C, Yu Z, Song X, Cao X (2006) The status and characteristics of eutrophication in the Yangtze River (Changjiang) Estuary and the Adjacent East China Sea, China. *Hydrobiologia,* **563**, 313-328.

Chang FH (1996) A review of knowledge of a group of closely related, economically important toxic *Gymnodinium/Gyrodinium* (Dinophyceae)species in new Zealand. *Journal of the Royal Society of New Zealand,* **26**, 381-394.

Chen Y, Yan T, Yu R, Zhou MJ (2011) Toxic effects of *Karenia mikimotoi* extracts on mammalian cells. *Chinese Journal of Limnology and Oceanography*, **29**, 860-868.

Cordell D, Drangert J-O, White S (2009) The story of phosphorous: Global food security and food for thought. *Global Environmental Change*, doi:10.1016/j.gloenvcha.2008.10.009.

Deeds J (2009) The evolving story of *Gymnodinium galatheanum* = *Karlodinium micrum* = *Karlodinium veneficum.* A ten year perspective. *Journal of Phycology,* 45, 1-2.

Dumont E, Harrison JA, Kroeze C, *et al.* (2005) Global distribution and sources of dissolved inorganic nitrogen export to the coastal zone: results from a spatially explicit, global model. *Global Biogeochemical Cycles*, 19, GB4S02.

Edwards M, Johns DG, Leterme SC, *et al.* (2006) Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnology and Oceanography*, **51**, 820-829.

Flynn KJ, Stoecker DK, Mitra A *et al.* (2013) Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research* **35**, 3-11.

Fu FX, Tatters AO, Hutchins DA (2012) Global change and the future of harmful algal blooms in the ocean. *Marine Ecology Progress Series*, **470**, 207-233.

Furuya K, Glibert PM, Zhou MJ *et al.,* eds. (2010) *GEOHAB Asia: Global ecology and oceanography of harmful algal blooms in Asia: A regional comparative programme.* IOC and SCOR, Paris and Newark, Delaware, 68 pp..

General Bathymetric Chart of the Oceans (GEBCO) (2013) http://www.bodc.ac.uk/projects/international/gebco/gebco_digital_atlas/.

Gleckler PJ, Taylor KE, Doutriaux C (2008) Performance metrics for climate models, *Journal of Geophysical Research*, **113(D6)**, D06104.

Glibert PM, Allen JI, Bouwman L *et al*. (2010) Modeling of HABs and eutrophication: status, advances, challenges. *Journal of Marine Systems*, 83, 262–275.

Glibert PM, Burkholder JM (2006) The complex relationships between increasing fertilization of the earth, coastal eutrophication and proliferation of harmful algal blooms. In: *Ecology of Harmful Algae* (eds Granéli E, Turner J) pp 341-354 Springer, Berlin Heidelberg.

Glibert PM, Burkholder JM (2011) Eutrophication and HABs: Strategies for nutrient uptake and growth outside the Redfield comfort zone. *Chinese Journal of Oceanology and Limnology,* **29**, 724-738.

Glibert PM, Burkholder JM, Kana TM (2012) Recent advances in understanding of relationships between nutrient availability, forms and stoichiometry and the biogeographical distribution, ecophysiology, and food web effects of pelagic and benthic *Prorocentrum* spp. *Harmful Algae,* **14**, 231-259.

Glibert PM, Harrison J, Heil CA, *et al.* (2006) Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochemistry,* **77**, 441-463.

Glibert PM, Kana TM, Brown K (2013) From limitation to excess: the consequences of substrate excess and stoichiometry for phytoplankton physiology, trophodynamics and biogeochemistry, and the implications for modeling. *Journal of Marine Systems* **125**, 14-28.

Glibert PM, Mayorga E, Seitzinger S (2008) *Prorocentrum minimum* tracks anthropogenic nitrogen and phosphorus inputs on a global basis: application of spatially explicit nutrient export models. *Harmful Algae,* **8**, 33-38.

Gómez F (2005) A list of free-living dinoflagellate species in the world's oceans. *Acta Botanica Croatia,* **64**, 129-212.

Granéli E, Flynn K (2006) Chemical and physical factors influencing toxin content. In: *Ecology of Harmful Algae* (eds Granéli E, Turner J) pp 229-241 Springer, Berlin Heidelberg.

Hajdu S, Edler L, Olenina L, *et al.* (2000) Spreading and establishment of the potentially toxic dinoflagellate *Prorocentrum minimum* in the Baltic Sea. *International Review of Hydrobiology,* **85**, 561-575.

Hajdu S, Pertola S, Kuosa H (2005) *Prorocentrum minimum* (Dinophyceae) in the Baltic Sea: morphology, occurrence – a review. *Harmful Algae*, **4**, 471-480.

Hardison DR, Sunda WG, Shea D, *et al.* (2013) Increased toxicity of *Karenia brevis* during phosphate limited growth: Ecological and evolutionary implications. PLoS ONE 8(3): e58545. doi:10.1371/journal.pone.0058545.

Harrison JH, Caraco NF, Seitzinger SP (2005). Global patterns and sources of dissolved organic matter export to the coastal zone: results from a spatially explicit, global model. *Global Biogeochemical Cycles,* **19**, GB4S04.

Heil CA, Glibert PM, Fan C (2005) *Prorocentrum minimum* (Pavillard) Schiller –A review of a harmful algal bloom species of growing worldwide importance. *Harmful Algae,* **4,** 449-470.

Heisler J, Glibert PM, Burkholder J *et al.* (2008) Eutrophication and harmful algal blooms: A scientific consensus. *Harmful Algae,* **8**, 3-13.

Hoagland P, Scatasta S (2006) The economic effects of harmful algal blooms. In: *Ecology of Harmful Algae* (eds Granéli E, Turner J) pp 393-401 Springer, Berlin Heidelberg.

Holt J, Harle J, Proctor R *et al.* (2009) Modelling the global coastal ocean, *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **367,** 939-951.

Holt JT, James ID (2001) An s coordinate density evolving model of the northwest European continental shelf 1, Model description and density structure. *Journal of Geophysical Research,* **106,** doi:10.1029/2000JC000304.

Hutchins DA, Mulholland MR, Fu FX (2009) Nutrient cycles and marine microbes in a CO_2-enriched ocean. *Oceanography*, **22**, 128-145.

Nakićenović N, Swart R (eds) (2000) *Special Report on Emissions Scenarios: A special report of Working Group III of the Intergovernmental Panel on Climate Change*, Cambridge University Press, ISBN 0-521-80081-1, 978-052180081-5 (pb: 0-521-80493-0, 978-052180493-6).

Jeong HJ, Yoo YD, Kim JS *et al.* (2010) Growth, feeding and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine planktonic food webs. *Ocean Science Journal,* **45,** 65-91.

Landsberg JH (2002) The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science,* **10,** 113-390.

Li AS, Stoecker DK, Coats DW (2000) Spatial and temporal aspects of *Gyrodinium galatheanum* in Chesapeake Bay: distribution and mixotrophy. *Journal of Plankton Research,* **22**, 2105-2124.

Li J, Glibert PM, Zhou M, *et al.* (2009) Relationships between nitrogen and phosphorus forms and ratios and the development of dinoflagellate blooms in the East China Sea. *Marine Ecology Progress Series,* **383,** 11-26.

Li J, Glibert PM, Zhou MJ (2010) Temporal and spatial variability in nitrogen uptake kinetics during harmful dinoflagellate blooms in the East China Sea. *Harmful Algae,* **9**, 531-539.

Lim PT, Usup G, Leaw CP (2012) Harmful algal blooms in Malaysian waters. *Sains Malaysiana*, **41**, 1509-1515.

Lou X, Huang W, Mao X, *et al.* (2006) Satellite observation of a red tide in the East China Sea during 2005. Remote Sensing of the Marine Environment, **6406**, doi: 10.1117/12.693856.

Lu D, Gobel J (2001) Five red tide species in genus *Prorocentrum* including the description of *Prorocentrum donghaiense* Lu sp. nov. from the East China Sea, China. *Chinese Journal of Oceanology and Limnology*, **19**, 337-344.

Lu D, Goebel J, Qi Y, *et al.* (2005). Morphology and genetic study of *Prorocentrum donghaiense* Lu from the East China Sea, and comparison with some related

Prorocentrum species. *Harmful Algae*, **4**, 493-506.

Lu D, Wang H, Huang H, *et al.* (2011) Morphological and genetic comparison of two strains of a *Prorocentrum* species isolated from Zhejiang coastal water of China and Masan Bay of Korea. *Chinese Journal of Oceanology and Limnology*, **29**, 832-839.

Marti O, Braconnot P, Bellier J *et al.* (2004) The new IPSL climate system model: IPSL-CM4 Note du Pole de Modélisation. 26, ISSN 1288-1619. Institut Pierre-Simon Laplace (IPSL).

Merino G, Barange M, Blanchard JL *et al.* (2012) Can marine fisheries and aquaculture meet fish demand from a growing human population in a changing climate? *Global Environmental Change,* doi:10.1016/j.gloenvcha.2012.03.003.

Nakićenović, N., Alcamo, J., Davis, G., de Vries, B., Fenhann, J., Gaffin, S., Gregory, K., Grübler, A., Jung, T. Y., Kram, T., Emilio la Rovere, E., Michaelis, L., Mori, S., Morita, T., Pepper, W., Pitcher, H., Price, L., Riahi, K., Roehrl, A., Rogner, H., Sankovski, A., Schlesinger, M., Shukla, P., Smith, S., Swart, R., van Rooyen, S., Victor, N., and Dadi, Z. (2000) Special report on emissions scenarios, Ipcc special reports, Cambridge University Press, Cambridge, 599 pp.

Olenina I Wasmund N, Hajdu S*, et al.* (2010) Assessing impacts of invasive phytoplankton: The Baltic Sea case. *Marine Pollution Bulletin,* **60,** 1691-1700.

Peñuelas J, Sardans J, Rivas-Ubach A *et al.* (2012) The human-induced imbalance between C,N and P in Earth's life system. *Global Change Biology*, **18**, 3-6.

Seitzinger SP, Harrison JA, Dumont E *et al.* (2005) Sources and delivery of carbon, nitrogen, and phosphorus to the coastal zone: An overview of Global Nutirent Export from Watersheds (NEWS) models and applications. *Global Biogeochemical Cycles*, **19**, GB4S01, doi:10.1029/2005GB002606.

Seitzinger SP, Mayorga E, Bouwman AF *et al.* (2010) Global river nutrient export: A scenario analysis of past and future trends. *Global Biogeochemical Cycles*, **23**, doi:10.1029/2009GB003587.

Sidharta BR (2005) The current status of research on harmful algal blooms in Indonesia. *Journal of Coastal Development,* **8**, 75-88.

Smayda TJ, Reynolds CS (2001) Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research,* **23**, 447-461.

Solomon S, Qin D, Manning M *et al*. (Eds.) (2007) *Climate Change 2007: The Physical Science Basis.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.

Sun J, Hutchins DA, Feng Y *et al.* (2011) Effects of changing pCO_2 and phosphate availability on domoic acid produciton and physiology of the marine harmful bloom diatom *Pseudo-nitzschia multiseries*. *Limnology and Oceanography*, **56**, 829-840.

Tang DL, Di BP, Wei GF, *et al.* (2006) Spatial, seasonal and species variations of harmful algal blooms in the South Yellow Sea and East China Sea. *Hydrobiologia*, **568**, 245–253.

Taylor KE (2001) Summarizing multiple aspects of model performance in a single diagram, *Journal of Geophysical Research*, **106(D7)**, 7183-7192.

Thoha H, Adnan Q, Sidabuta T *et al.* (2007) Note on the occurrence of phytoplankton and its relation with mass mortality in the Jakata Bay, May and Novemebr 2004. *Maraka, Sains,* **11**, 63-67.

Vargo GA, Heil CA, Fanning KA *et al.* (2008) Nutrient availability in support of *Karenia brevis* blooms in the central West Florida Shelf: What keeps *Karenia* blooming? *Continental Shelf Research* **28,** 73-98.

Wang J, Wu J (2009) Occurrence and potential risks of harmful algal blooms in the East China Sea. *Science of the Total Environment*, **407**, 4012-4021.

Zhang H, Litaker W, Vandersea MW, Tester P, Lin SJ (2008) Geographic distribution of *Karlodinium veneficum* in the US east coast as detected by ITS-ferredoxin real-time PCR assay. *Journal of Plankton Research*, **30**:905-922.

Zhou MJ, Shen ZL, Yu RC (2008) Responses of a coastal phytoplankton community to increased nutrient input from the Changjiang (Yangtze) River. *Continental Shelf Research,* **28**, 1483-1489.

Zhou MJ, Yan T, Zou J (2003) Preliminary analysis of the characteristics of red tide areas in Changjiang River estuary and its adjacent sea. *Chinese Journal of Applied Ecology*, **14**, 1031–1038.

Table 1: Mean bias errors in each domain for Chlorophyll (µabl^{-1}), Sea Surface Temperature (SST, ^{o}C) and Sea Surface Salinity (SSS, PSU). RA and PD refer to the re-analysis and present day forced simulations.

	Chl (RA)	Chl (PD)	SST (RA)	SST (PD)	SSS (RA)	SSS(PD)
NW Europe	0.95	1.05	0.23	-2.12	-0.10	0.47
NE Asia	2.36	2.27	0.24	-3.01	-0.15	-0.43

Table 2: Physiological “rules” defining the physical and chemical envelope where the two phytoplankton genera, *Prorocentrum* spp. and *Karenia* spp. may flourish. Data were largely derived from syntheses provided in Heil *et al.* (2005), Glibert *et al.* (2012), Vargo *et al.* (2008) and Brand *et al.* (2012). (SST: Sea Surface Temperature (ºC); SSS: Sea Surface Salinity; NH_4: ammonium concentration (mmol-N/m^3); NO_3: nitrate concentration (mmol-N/m^3); N: dissolved inorganic nitrogen concentration (mmol-N/m^3); P: dissolved inorganic phosphorus concentration (mmol-P/m^3))

		Prorocentrum-type	*Karenia*-type
Physical niche	temperature	$15<SST<25$	$20<SST<30$
	salinity	$11<SSS<33$	$11<SSS<33$
Chemicalniche		$NH_4>NO_3$	$NH_4>NO_3$
Potential toxicity		$N:P<5.33$ or $N:P>48$	$N:P<5.33$ or $N:P>48$

Table3. Results of the analysis of percent changes in habitat suitability of the three regions when individual parameters are changed separately or in varying combination for each HAB genera. The first line gives the reference run for all parameters set at present day (p.d.) conditions. Subsequent lines illustrate the change relate to the reference run when one or more parameters is altered to the future condition (A1B scenario). The values represent the total number of times in the model run when all three conditions suitable for the HAB genera are met, normalized to the total number of pixels in the domain in a 120 month period (10 years of present day). Subsequent lines show the percent change relative to this reference run.

	Parameter and model scenario			*Prorocentrum* Spp.			*Karenia* Spp.	
Salinity	Temperature	Nutrient ratio	NW European	NE Asia	SE Asia	NW European	NE Asia	SE Asia
p.d.	p.d.	p.d.	0.48	3.51	0.10	0.01	1.62	1.27
p.d.	p.d.	A1B	-10.1 %	-18.6 %	-15.3 %	-84.4 %	-21.8 %	-13.9 %
p.d.	A1B	p.d.	335.7 %	14.2 %	-32.3 %	2716.6 %	115.4 %	-81.9 %
p.d.	A1B	A1B	262.8 %	-2.0 %	-39.0 %	1934.1 %	74.5 %	-84.4 %
A1B	p.d.	p.d.	94.1 %	-10.8 %	-4.1 %	100.6 %	-7.1 %	16.1 %

A1B	p.d.	A1B	55.8 %	-26.2 %	-18.1 %	-81.6 %	-26.6 %	-0.9 %
A1B	A1B	p.d.	821.3 %	-2.1 %	-31.9 %	3860.9 %	95.3 %	-80.6 %
A1B	A1B	A1B	694.4 %	-15.8 %	-39.1 %	2183.7 %	59.3 %	-83.6 %

Figure legends

Figure 1. Schematic representation of the coupled oceanographic- biogeochemical ERSEM model.

Figure 2. Multi-domain, multi-forcing Taylor diagrams of Sea Surface Temperature (SST), Sea Surface Salinity (SSS) and Chlorophyll for the NW European and NE Asia regions. The REF point refers to the observational data (Reynolds SST, World Ocean Atlas Salinity and SeaWifs derived chlorophyll). Each coloured dot represents a re-analysis forced model domain and triangle the corresponding present-day forced simulation. The contour lines are an arbitrary indication of model skill as defined by Glecker *et al.* (2008). Note that errors are normalised relative to the observed standard deviation and that the time-mean, spatial-mean (overall model bias) has been removed from each field prior to error quantification.

Figure3. Comparison of output of the coupled oceanographic-biogeochemical model described in text for the NE European/Baltic Sea region. Panels (a) and (b) depict the spatial distribution of habitat suitability (spatially-explicit fraction of time of year for which all suitable conditions were met) for *Prorocentrum* spp. for present (encompasses period from 1980-1990) and future conditions projected using A1B IPCC scenarios for climate change

(encompasses period from 2090-2100) and panel (c) represents the difference between present and future conditions. Panels (d-f) are the same except for conditions suitable for *Karenia* spp.

Figure 4. As for Figure 3, except for NE Asia.

Figure 5. As for Figure 3 except for SE Asia.

Figure 6. Comparison of output of the coupled oceanographic-biogeochemical model for the NW European/Baltic Sea region, future condition (panels a,b), and NE Asia, present day condition (panels c,d) depicting the fraction of months of the year suitable for growth of *Karenia*-type HAB species (panels a,c) and the percentage of those months also conducive to a toxic condition (panels b,d).

Figure 7. Panel (a) Comparison of impacts of blooms of *Prorocentrum minimum* in various Baltic Sea sub-basins, as assessed using a biopollution scale described by Olenina *et al.* (2010). Figure reproduced from Olenina *et al.* (2010) with permission of Elsevier.
Panels (b) Distribution of *Prorocentrum* spp. (log (x+1) cell counts) in the post 1990s era and Panel (c), the anomaly of the distribution of this HAB species in the post-1990s era relative to the long-term mean (1960s-post 1990s). Panels (b) and (c) are from Edwards *et al.* (2006) used with permission of the Association for the Sciences of Limnology and Oceanography. Note the similarity between Figure 7a and 7b and Figure 3a.

Figure 8. Panel (a) False color image of the East China Sea on 29 May 2005 acquired byMODIS Terra showing the distribution of a bloom of pelagic *Prorocentrum donghaiense*. Image reproduced from Lou et al. (2006) with permission of the International Society of

Optical Engineering. Panels (b)-(e) represent SEAWIFS images for the Yellow and Bohai Seas during spring (1999-2002) converted to a red tide index chlorophyll algorithm developed from bio-optical data from native HAB species (scale represents Red tide Chlorophyll Algorithm, RCA, index). Image is from Ahn & Shannmugam (2006) used with permission of the publisher (Elsevier). Note the similarity between Figures 8a and 8e and Figure 4a.

Figure 9. Panels (a,b): Comparison of frequency diagrams, by month of the year for suitability of physical and nutrient conditions for *Prorocentrum*-type HABs in northern European coast under present conditions (a) and under the future scenario (b) described in text. The frequency diagrams depict the fraction of pixels in the ERSEM model that meet the criteria by month. Panels (c,d): spatial extension of the physical (salinity and temperature; red) and nutrient ($NH_4^+ > NO_3^-$; green) niche and both conditions overlapping (brown) for the month of July under present conditions (year 2001; panel c) and under the future scenario (year 2100; panel d) described in text. Where neither condition is verified, the map domain is white. The regions of the maps indicated in blue are outside the model domain.