

Original article

Climate change and harmful algal blooms in the North Sea

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Abstract

The projected effect of climate change for the year 2100 in the coastal zone of The Netherlands, a 4 °C temperature rise and increased salinity stratification, on the growth rates of six harmful and two non-harmful phytoplankton species was investigated in batch laboratory cultures. Stratification can split the mixed water column (18 °C, 150 W h m⁻² per day) into a bottom (18 °C, 10 W h m⁻² per day) and surface layer (22 °C, 600 W h m⁻² per day); these three conditions (the present scenario) were compared to a 2100 scenario in which temperatures were increased by 4 °C. The growth rates of the two non-harmful species, the diatom *Skeletonema costatum* and the cryptophyte *Rhodomonas* sp. did not significantly change from present-mixed to 2100-surface conditions. Two harmful species, the prymnesiophyte *Phaeocystis globosa* and the diatom *Pseudo-nitzschia multiseries*, died rapidly at the 2100-surface conditions. On the other hand, two dinoflagellates (*Prorocentrum micans* and *Prorocentrum minimum*) and two raphidophytes (*Fibrocapsa japonica* and *Chattonella antiqua*) doubled their growth rates at 2100-surface conditions compared to present-mixed conditions. Given the restrictions set by the experiment, the uncertainties in climate change projections as well as the effects of climate change on the marine ecosystem, the qualitative conclusion from this investigation is that the risk of harmful dinoflagellate and raphidophyte blooms will increase rather than decrease due to climate change.

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Keywords: Climate change; Temperature; Stratification; Harmful algal blooms; HAB; North Sea; Phytoplankton; *Prorocentrum micans*; *Prorocentrum minimum*; *Chattonella antiqua*; *Fibrocapsa japonica*; *Phaeocystis globosa*; *Pseudo-nitzschia multiseries*; *Rhodomonas* sp.; *Skeletonema costatum*

1. Introduction

The global change in climate between 1990 and 2100 leads to a projected rise in temperature of 1.4–5.8 °C with a 90% probability interval of 1.7–4.9 °C (IPCC, 2001; Wigley and Raper, 2001). A direct consequence of global warming is thermal expansion of water, and hence a rise in sea level in 2100 by 0.1–0.9 m (IPCC, 2001). In low countries as The Netherlands, coastal zone managers are concerned by the rise in sea level because the risk of flooding increases. Another concern is how the rise in seawater temperature will affect biodiversity, the functioning of the marine ecosystem and valuable ecosystem services such as fisheries. However, ecosystems are very complex and their responses to large changes in maximum temperature are difficult to predict theoretically.

Photosynthesis and phytoplankton growth are basic processes to the marine ecosystem, and in general both rates double when temperature increases by 10 °C (Eppley, 1972; Raven and Geider, 1988). However, this so-called $Q_{10} = 2$

rule cannot be applied rigorously because many phytoplankton species, and even whole taxonomic groups, are adapted to grow only within certain temperature ranges (Smayda, 1980). In the Southern Bight of the North Sea where temperature ranges from 0 °C in winter to 22 °C in summer (Cadée, 1991; Peperzak et al., 1996), the species succession is from small diatoms in spring to large diatoms and dinoflagellates in summer, while cryptophytes and blooms of the prymnesiophyte *Phaeocystis globosa* occur in both seasons (Bakker et al., 1990; Cadée and Hegeman, 1986; Gieskes and Kraay, 1975; Hofstraat et al., 1994; Kat, 1992; Peperzak et al., 1996; Peperzak, 2002). The Dutch coastal zone is economically important to the shellfish industries, fisheries and tourism. Therefore, the development in this area of harmful algal blooms (HABs) is of particular concern. Recurrent HAB species are the dinoflagellates *Dinophysis acuminata*, *Prorocentrum minimum* and the diatom *Pseudo-nitzschia multiseries* (potential producers of shellfish toxins), the raphidophytes *Fibrocapsa japonica*, *Chattonella marina*, *Chattonella antiqua* (toxic to fish) and *P. globosa* (producer of foam). The main bloom periods of these species are in late spring or summer (Kat, 1992; Peperzak et al., 1996; Vrieling et al., 1995; Vrieling et al., 1996), implying

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that they grow well at relatively high temperatures. This is certainly the case for *F. japonica*, *C. marina* and *C. antiqua* that have temperature optima in vitro at 25 °C (Khan et al., 1995; Khan et al., 1996; Khan et al., 1998; Nakamura and Watanabe, 1983). Therefore, it is not improbable that a rise in maximum seawater temperature in the 21st century is beneficial to these harmful raphidophytes.

The projected change in climate will also lead to alterations in the geographic distribution and intensity of precipitation (IPCC, 2001). In temperate regions of the northern hemisphere, such as Britain, this means an increase in extreme precipitation events (Jones and Reid, 2001). The water flow in the river Rhine at the German-Dutch border will become less dependant on snow melt and more dependant on rainfall, leading to increased discharges in most International Panel on Climate Change (IPCC) scenarios for 2100 (Kwadijk, 1993). Even at present the river Rhine delivers pulses of freshwater into the Dutch coastal zone of the North Sea, leading to intermittent salinity stratification in an area extending 30–40 km offshore and 100 km along the coast towards the north (de Ruijter et al., 1997; van Alphen et al., 1988; van der Giessen et al., 1990).

During salinity stratification in the Dutch coastal zone, the phytoplankton in the shallow (3–5 m) surface layer not only experiences a decrease in salinity, but also rapid increases in daily irradiance and water temperature (Peperzak et al., 1996). It has been shown that stratification in this region is conducive to blooms of *P. globosa* and *D. acuminata* (Peperzak, 1993; Peperzak et al., 1996). However, experiments on the combined effect of stratification and temperature rise on the growth of HAB species have not yet been performed. This combined effect could be calculated using autecological data from the literature but such data, especially in the higher temperature range above 20 °C, are not readily available. Furthermore, experimental differences between autecological studies make it difficult to directly estimate and compare the growth rates of several species. Therefore, an experimental approach was chosen.

Assuming a high estimate of temperature change in Europe of 4 °C in 2100 (Können, 2001), and at least the same intensity of summer salinity stratification in the Dutch coastal zone as present, the relevant changes in salinity, temperature and daily irradiance on phytoplankton growth rates were investigated in batch cultures under nutrient-replete conditions. Emphasis was placed on harmful algae

because of their economical relevance, environmental impact, and because a rise in temperature appeared to be conducive to the formation of HABs.

2. Materials and methods

Daily irradiance calculations were made using data from Nw10 (52°18'N, 4°18'E), a representative monitoring station in the Dutch coastal zone (Peperzak et al., 1998). Mean August values (1991–2000) of salinity (31 psu) and suspended matter (4 mg l⁻¹), were used to calculate an irradiance attenuation coefficient $K_d = 0.65 \text{ m}^{-1}$ (Peperzak et al., 1998). Using a mean surface daily irradiance (DI, as PAR) of 1700 W h m⁻² per day (mean value of July and August, 1989–1999), the DI per meter water column was calculated for three conditions: (i) a completely mixed water column ($z = 19 \text{ m}$), (ii) a surface mixed layer ($z = 0–4 \text{ m}$) and (iii) a bottom mixed layer ($z = 5–19 \text{ m}$) (Peperzak, 1993). The results are shown in Table 1. Assuming that algae do not grow at irradiance values less than 1 W m⁻², day-length under each condition was calculated as: (i) 14:40, (ii) 15:10 and (iii) 4:40 (h per day). Next, the irradiances (W m⁻²) for three identical Sanyo-Gallenkamp incubators were calculated by dividing the calculated daily irradiance (W h m⁻² per day) by day-length (h per day). The incubators were equipped with Philips TLD 30W84o (cool white) tubes. Irradiance was measured in the culture flasks with a Photodyne XLA photometer equipped with a spherical sensor.

Two scenarios were investigated: the “present” and “2100” (Table 1). The first scenario assumes present day seawater temperatures of the mixed water column (18 °C), and instantaneous stratification and a concomitant rise in daily irradiance, and temperature to 22 °C (Peperzak et al., 1996). The second scenario assumes the same conditions, but with an overall 4 °C rise in seawater temperature (Können, 2001). During the experiment the phytoplankton species (see below) were cultured under “mixed” conditions, diluted with fresh medium, then subcultured directly under “surface” and “bottom” conditions (Table 1). Because the temperatures in the incubators could not be regulated accurately, the means of values measured inside culture vessels are listed in Table 1 as well.

The effect of salinity differences (29 and 31 psu) on growth rates was examined in a separate experiment using

Table 1

Experimental design. As a result of stratification the mixed water column splits into a surface and a bottom layer. Two scenarios were tested. Conditions in the present scenario are derived from 1989 to 2000 summer values in the Dutch coastal zone of the North Sea. In the 2100 scenario the conditions are identical with the exception of temperature (+4 °C). The temperatures measured inside the culture vessels deviated maximally by 0.5 °C from set values

Scenario	Condition	Salinity (psu)	E (W h m ⁻² per day)	Temperature set (°C)	Temperature measured (°C)
Present	Mixed	31	150	18	17.5
Present	Surface	29	600	22	21.5
Present	Bottom	31	10	18	18.5
2100	Mixed	31	150	22	22
2100	Surface	29	600	26	25.5
2100	Bottom	31	10	22	22

Table 2
List of phytoplankton species

Species	Family	Clone
<i>P. micans</i>	Dinophyceae	CCMP1589
<i>P. minimum</i>	Dinophyceae	BAHME66
<i>C. antiqua</i>	Raphidophyceae	CaKA84
<i>F. japonica</i>	Raphidophyceae	FjW420
<i>P. globosa</i>	Prymnesiophyceae	Ph91 (*)
<i>P. multiseriis</i>	Bacillariophyceae	Md0913Psn6
<i>Rhodomonas</i> sp.	Cryptophyceae	R. Duin
<i>S. costatum</i>	Bacillariophyceae	CCMP1332

(*) Solitary, non-flagellate cells.

the species in Table 2 (with the exception of *P. multiseriis* and *C. antiqua*) at 500 W h m⁻² per day, 18 °C and *L* = 14 h per day.

Six HAB species and the non-harmful *Skeletonema costatum* and *Rhodomonas* sp. (Table 2) were grown in Erlenmeyer flasks under nutrient-replete conditions in 100 ml PEP medium, made from natural seawater with a salinity of 31 psu (Peperzak et al., 2000). *Prorocentrum micans* is used as a proxy for *D. acuminata*, a dinoflagellate that cannot be cultured (Peperzak et al., 1996). Demineralized water was used to make 29 psu seawater. Biomass was measured at least three times per week as in vivo fluorescence (Fv) on a Hitachi F2000 spectrofluorometer ($\lambda_{\text{ex}} = 435$ nm, $\lambda_{\text{em}} = 683$ nm). Growth rates were calculated from linear regression on $\ln F_v$, measured during exponential growth ($\mu = (\ln F_t - \ln F_0)/(t - t_0)$ per day). Flow cytometry showed that the transient effect on in vivo fluorescence, caused by the rapid transfer of the cells to “surface” and “bottom” conditions, stabilized within 2 d and, therefore, did not influence growth rate measurements. In all scenarios, growth rates under each condition were measured at least twice.

3. Results

3.1. Effect of salinity on growth rate

Growth rates of four harmful and two non-harmful species at 29 psu were not significantly different from growth rates at 31 psu (Fig. 1). This means that in the main experiment, the additional effect of decreased salinity on growth rates under “surface” conditions may be neglected.

3.2. Growth rates in the present and 2100 scenarios

Under present mixed conditions all species grew well with growth rates ranging from 0.33 and 0.35 per day (the large species *P. micans* and *C. antiqua*) to 1.12 and 1.14 per day (the small species *S. costatum* and *P. globosa*; Table 3). With the exception of *P. globosa*, growth rates increased under surface conditions, but they became practically zero after transfer to the low-bottom-daily irradiance.

An increase of 4 °C did not considerably change mixed growth rates except in *P. globosa* (– 32%), and in *P. multi-*

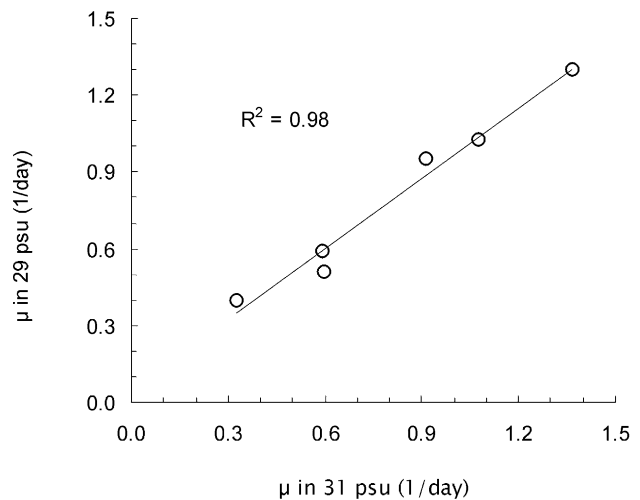


Fig. 1. Growth rates (per day) of six phytoplankton species at salinities of 29 and 31 psu. The line is calculated by linear regression.

series that died rapidly at all temperatures ≥ 22 °C. High irradiance–high temperature surface conditions also led to the death of *P. globosa*. In the 2100 scenario the surface growth rates of the non-harmful species *Rhodomonas* sp. and *S. costatum* did not differ much from present mixed conditions. On the other hand, the 2100 surface growth rates of the dinoflagellates *P. micans* and *P. minimum* and the raphidophytes *C. antiqua* and *F. japonica* doubled compared to the present mixed conditions (Table 3). The effect of a temperature rise and stratification is especially clear, when mixed and surface growth rates in both scenarios are presented relative to the present mixed conditions (Figs. 2 and 3). Enhanced daily irradiance as well as rises in temperature led to stepwise increases in the dinoflagellates’ and raphidophytes’ growth rates (Fig. 2a–d). In contrast, two other harmful species, *P. globosa* and *P. multiseriis*, had reduced growth rates or died in the 2100 scenario (Fig. 3a–b). A 4 °C rise under mixed conditions led to increased growth rates of *Rhodomonas* sp. and *S. costatum*, but growth rates decreased under surface conditions in the 2100 scenario (Fig. 3c–d).

4. Discussion

Global climate change expressed as an increase of the summer temperature maximum by 4 °C in 2100, in combination with water column stratification, led to a doubling of growth rates of potentially harmful dinoflagellates and raphidophytes. This means that the risk of HABs by these species increases considerably. At present, blooms of *D. acuminata* (and its proxy *P. micans*), *P. minimum*, *F. japonica* and *C. antiqua* are observed more or less regularly in the Dutch coastal zone of the North Sea (Kat, 1992; Peperzak et al., 1996; Vrieling et al., 1995; Vrieling et al., 1996). Therefore, the frequency and intensity of blooms by these species may increase in the future.

Table 3

Growth rates (μ in per day; duplicate means \pm standard deviation (S.D.)) of eight phytoplankton species under two climate scenarios: present and 2100 (+4 °C) under mixed and stratified conditions (surface and bottom). † means: cells died rapidly

Species	Present			2100		
	Mixed	Surface	Bottom	Mixed	Surface	Bottom
<i>P. micans</i>	0.35 \pm 0.07	0.41 \pm 0.04	0.07 \pm 0.10	0.39 \pm 0.03	0.75 \pm 0.27	– 0.05 \pm 0.04
<i>P. minimum</i>	0.49 \pm 0.05	0.84 \pm 0.01	– 0.02 \pm 0.06	0.55 \pm 0.02	1.02 \pm 0.22	0.01 \pm 0.11
<i>C. antiqua</i>	0.33 \pm 0.07	0.54 \pm 0.08	– 0.09 \pm 0.04	0.44 \pm 0.05	0.70 \pm 0.11	– 0.06 \pm 0.04
<i>F. japonica</i>	0.44 \pm 0.05	0.73 \pm 0.02	– 0.03 \pm 0.02	0.58 \pm 0.04	0.89 \pm 0.10	– 0.03 \pm 0.01
<i>P. globosa</i>	1.14 \pm 0.06	0.72 \pm 0.15	– 0.02 \pm 0.03	0.77 \pm 0.05	†	– 0.03 \pm 0.16
<i>P. multiseriis</i>	1.03 \pm 0.11	1.63 \pm 0.31	0.04 \pm 0.04	†	†	†
<i>Rhodomonas</i> sp.	0.70 \pm 0.22	0.98 \pm 0.02	0.03 \pm 0.02	1.14 \pm 0.27	0.89 \pm 0.06	– 0.05 \pm 0.02
<i>S. costatum</i>	1.12 \pm 0.05	1.86 \pm 0.04	0.10 \pm 0.03	1.23 \pm 0.13	1.15 \pm 0.26	– 0.04 \pm 0.15

However, due to several uncertainties it is difficult to quantify the chance of a dinoflagellate–raphidophyte HAB increase in the 21st century. In the first place, the increases in temperature and precipitation are projections, based on a range of scenarios (IPCC, 2001; Können, 2001; Wigley and Raper, 2001). Secondly, the expected changes in Rhine discharge and North Sea stratification also depend on regional scenarios involving land use in the catchment area (Kwadijk, 1993). The present climate situation leads to an optimum water mass exchange in the North Sea and a relatively rapid dilution of anthropogenic pollution such as phytoplankton nutrients (Backhaus, 1989). Due to climate change, the flushing of the North Sea may become less rapid (Blaas et al., 2001), leading to increased nutrient concentrations and a situation that can be regarded as more beneficial to the formation of HABs. Finally, difficulties in assessing the

chance of an increased HAB occurrence lie in predicting the in situ behavior of the phytoplankton and the overall ecosystem response to the proposed forcings (temperature and stratification).

Prediction of the ecosystem response is difficult for a number of reasons. It is obvious that an increase in seawater temperature not only affects the phytoplankton growth rate, but also the physical environment to which the cells are subjected. Several processes are strongly affected by temperature change. Increased temperature leads to a considerably decreased viscosity (Vogel, 1996), which theoretically leads to increased: (i) nutrient diffusion towards the cell surface, important when interspecific competition for nutrients takes place, and (ii) sedimentation rates, which will be important for non-flagellate species such as diatoms.

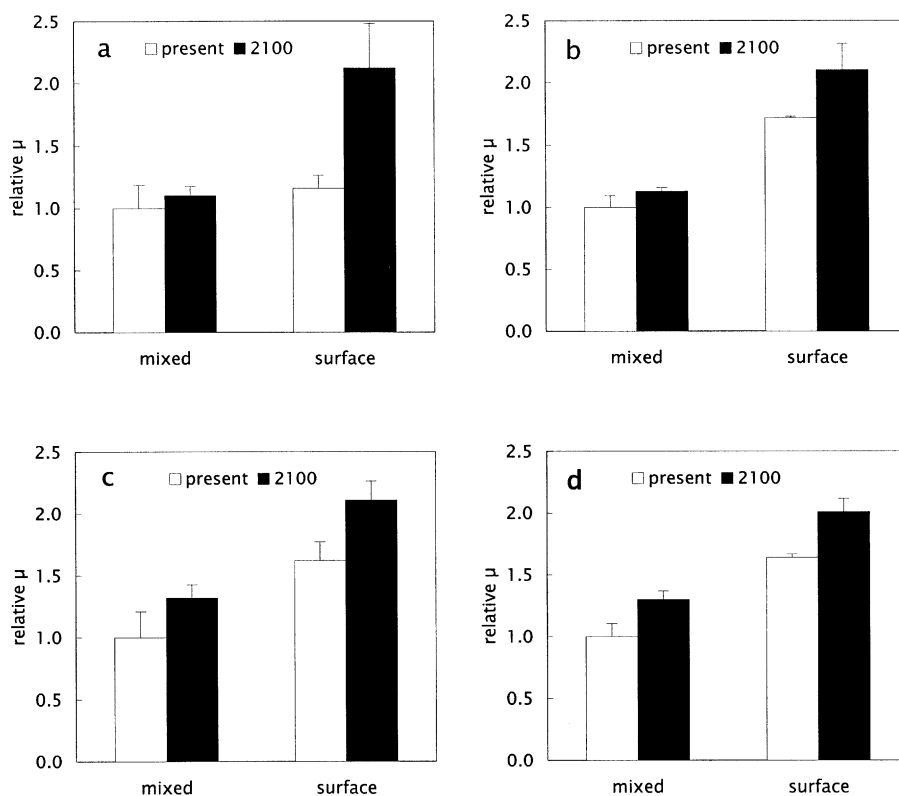


Fig. 2. Mean growth rates (\pm S.D.) of *P. micans* (a), *P. minimum* (b), *F. japonica* (c) and *C. antiqua* (d) under 2100-mixed, present-surface and 2100-surface conditions relative to the growth rate under present mixed conditions ($\mu_{\text{relative}} = 1$).

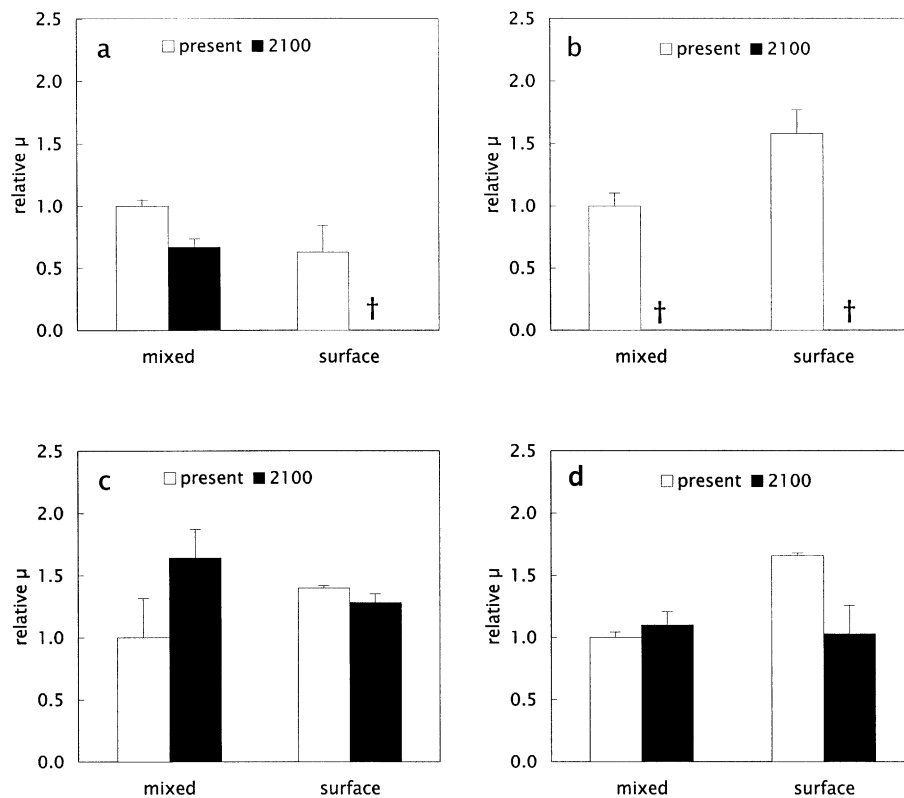


Fig. 3. Mean growth rates (\pm S.D.) of *P. globosa* (a), *P. multiseriis* (b), *Rhodomonas* sp. (c) and *S. costatum* (d) under 2100-mixed, present-surface and 2100-surface conditions relative to the growth rate under present mixed conditions ($\mu_{\text{relative}} = 1$). †, cells died rapidly.

One trophic level up, zooplankton metabolic rates have a Q_{10} of nearly 2 (Ikeda, 1985) so that ingestion of phytoplankton will increase at elevated temperatures. The simultaneous decrease of seawater viscosity could mean that filter-feeding animals become able to catch larger particles (Vogel, 1996). This would mean that relatively larger cells become more susceptible to grazing. On the other hand, *P. micans*, *C. antiqua* and *F. japonica* are large species compared to *Rhodomonas* sp. and *S. costatum*, and size combined with the ability to produce toxic compounds offer protection against micro- and meso-zooplankton grazers (Kamiyama and Arima, 2001; Turner et al., 1998).

Summarizing the discussion, the projected increases in temperature and in precipitation associated with climate change fall into wide ranges and uncertainties exist in their effect on stratification and North Sea flushing. Furthermore, the scenarios tested in the present investigation could not take into account the effects of temperature and stratification changes on ecological processes that are important in phytoplankton species succession in situ. On the other hand, the growth rates of the dinoflagellates and raphidophytes tested doubled as a result of simulated climate change. Therefore, without making a quantitative assessment, the main conclusion is that due to climate change the risk of harmful dinoflagellate and raphidophyte blooms in the Dutch coastal zone will increase rather than decrease.

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References

- Backhaus, J.O., 1989. The North Sea and the climate. *Dana* 8, 69–82.
- Bakker, C., Herman, P.M.J., Vink, M., 1990. Changes in seasonal succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (SW Netherlands). *J. Plankton Res.* 12, 947–972.
- Blaas, M., Kerkhoven, D., de Swart, H.E., 2001. Large-scale circulation and flushing characteristics of the North Sea under various climate forcing. *Climate Res.* 18, 47–54.
- Cadée, G.C., Hegeman, J., 1986. Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophyceae) in the western-most inlet of the Wadden Sea during the 1973 to 1985 period. *Neth. J. Sea Res.* 20, 29–36.
- Cadée, G.C., 1991. *Phaeocystis* colonies overwintering in the water column? *Neth. J. Sea Res.* 28, 227–230.

- de Ruijter, W.P.M., Visser, A.W., Bos, W.G., 1997. The Rhine outflow: a prototypical pulsed discharge plume in a high energy shallow sea. *J. Mar. Syst.* 12, 263–276.
- Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* 70, 1063–1085.
- Gieskes, W.W.C., Kraay, G.W., 1975. The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Neth. J. Sea Res.* 9, 166–196.
- Hofstraat, J.W., van Zeijl, W.J.M., de Vreeze, M.E.J., Peeters, J.C.H., Peperzak, L., Colijn, F., Rademaker, M., 1994. Phytoplankton monitoring by flow cytometry. *J. Plankton Res.* 16, 1197–1224.
- Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* 85, 1–11.
- IPCCA report of working group I of the Intergovernmental Panel on Climate Change. Summary for Policymakers and Technical Summary. <http://www.ipcc.ch/pub/>.
- Jones, P.D., Reid, P.A., 2001. Assessing future changes in extreme precipitation over Britain using a regional climate model integrations. *Int. J. Clim.* (in press).
- Kamiyama, T., Arima, S., 2001. Feeding characteristics of two tintinnid ciliate species on phytoplankton including harmful species: effects of prey size on ingestion rates and selectivity. *J. Exp. Mar. Biol. Ecol.* 257, 281–296.
- Kat, M., 1992. Year-to-year variation in the occurrence of some dominant phytoplankton species in Dutch coastal waters, 1973–1984. *Hydrobiol. Bull.* 25, 225–231.
- Khan, S., Arakawa, O., Onoue, Y., 1995. Effects of physiological factors on morphology and motility of *Chattonella antiqua* (Raphidophyceae). *Bot. Mar.* 38, 347–353.
- Khan, S., Arakawa, O., Onoue, Y., 1996. Growth characteristics of a neurotoxin-producing chloromonad *Fibrocapsa japonica* (Raphidophyceae). *J. World Aquaculture Soc.* 27, 247–253.
- Khan, S., Arakawa, O., Onoue, Y., 1998. Physiological investigations of a neurotoxin-producing phytoflagellate, *Chattonella marina* (Raphidophyceae). *Aquaculture Res.* 29, 9–17.
- Können, G.P., 2001. Climate scenarios for impact studies in The Netherlands. Royal Netherlands Meteorological Institute (KNMI). De Bilt, The Netherlands p. 6.
- Kwadijk, J., 1993. The impact of climate change on the discharge of the River Rhine. Ph.D. thesis, University of Utrecht.
- Nakamura, Y., Watanabe, M.M., 1983. Growth characteristics of *Chattonella antiqua* (Raphidophyceae). Part 1. Effects of temperature, salinity, light intensity and pH on growth. *J. Oceanogr. Soc. Japan* 39, 110–114.
- Peperzak, L., 1993. Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae). *J. Plankton Res.* 15, 809–821.
- Peperzak, L., Snoeijer, G.J., Dijkema, R., Gieskes, W.W.C., Joordens, J., Peeters, J.C.H., Schol, C., Vrieling, E.G., Zevenboom, W., 1996. Development of a *Dinophysis acuminata* bloom in the river Rhine plume (North Sea). In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*. UNESCO, Paris, pp. 273–276.
- Peperzak, L., Colijn, F., Gieskes, W.W.C., Peeters, J.C.H., 1998. Development of the diatom—*Phaeocystis* spring bloom in the Dutch coastal zone (North Sea): the silicon depletion versus the daily irradiance hypothesis. *J. Plankton Res.* 20, 517–537.
- Peperzak, L., Duin, R.N.M., Colijn, F., Gieskes, W.W.C., 2000. Growth and mortality of flagellates and non-flagellated cells of *Phaeocystis globosa* (Prymnesiophyceae). *J. Plankton Res.* 22, 107–119.
- Peperzak, L., 2002. The wax and wane of *Phaeocystis globosa* blooms. Ph.D. thesis, University of Groningen.
- Raven, J.A., Geider, R.J., 1988. Temperature and algal growth. *New Phytol.* 110, 441–461.
- Smayda, T., 1980. Phytoplankton species succession. In: Morris, I. (Ed.), *The Physiological Ecology of Phytoplankton*. Blackwell Scientific Publications, Oxford, pp. 493–570.
- Turner, J.T., Tester, P.A., Hansen, P.J., 1998. Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In: Erson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer, Berlin, pp. 453–474.
- van Alphen, S.J.L.J., de Ruijter, W.P.M., Borst, J.C., 1988. Outflow and three-dimensional spreading of Rhine river water in the Netherlands coastal zone. In: Dronkers, J., van Leussen, W. (Eds.), *Physical Processes in Estuaries*. Springer, Berlin, pp. 70–92.
- van der Giessen, A., de Ruijter, W.P.M., Borst, J.C., 1990. Three-dimensional current structure in the Dutch coastal zone. *Neth. J. Sea Res.* 25, 45–55.
- Vogel, S., 1996. *Life in Moving Fluids*. Princeton University Press, Princeton.
- Vrieling, E.G., Koeman, R.P.T., Nagasaki, K., Ishida, Y., Peperzak, L., Gieskes, W.W.C., Veenhuis, M., 1995. *Chattonella* and *Fibrocapsa* (Raphidophyceae): first observations of, potentially harmful, red tide organisms in Dutch coastal waters. *Neth. J. Sea Res.* 33, 183–191.
- Vrieling, E.G., Koeman, R.P.T., Scholin, C.A., Scheerman, P., Peperzak, L., Veenhuis, M., Gieskes, W.W.C., 1996. Identification of a domoic acid-producing *Pseudonitzschia* species (Bacillariophyceae) in the Dutch Wadden Sea with electron microscopy and molecular probes. *Eur. J. Phycol.* 31, 333–340.
- Wigley, T.M.L., Raper, S.C.B., 2001. Interpretation of high projections for global-mean warming. *Science* 293, 451–454.