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Do the polyunsaturated aldehydes produced by *Phaeocystis pouchetii* (Hariot) Lagerheim influence diatom growth during the spring bloom in Northern Norway?

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The marine bloom-forming phytoplankter Phaeocystis pouchetii (Prymnesiophyceae) *is known to produce and release the cytotoxic* $\alpha,\beta,\gamma,\delta$*-unsaturated aldehyde 2-*trans*-4-*trans*-decadienal (DD), known to inhibit mitotic cell divisions in several different cell types. The possible allelopathic effects of DD on monocultures of three common diatoms from the coastal waters of northern Norway were assessed. The results showed that division rates for all three diatom species (*Skeletonema costatum, Chaetoceros socialis *and* Thalassiosira antarctica*) decreased as concentration of DD increased. Furthermore field data from the spring bloom in Vestfjorden (2000 and 2001) were analysed to examine whether the presence of* P. pouchetii *influences other species adversely. Our data revealed no significant adverse effect of* P. pouchetii *on diatom presence since diatom diversity generally was positively correlated to* P. pouchetii *biomass. The year with the lowest amounts of* P. pouchetii *had the lowest diversities, and the diatom species composition and abundance was comparable to situations where* P. pouchetii *was either absent or present in minute amounts. At some instances low diversity co-occurred with large fractions of* P. pouchetii*, but since this were at the strongest vertical mixing we believe this to be a result of physical control.* P. pouchetii *and* S. costatum *were the most frequently co-occurring species, and since they are both known producers of polyunsaturated aldehydes we cannot exclude the possibility that the presence of DD released from* P. pouchetii *induced by heavy grazing might influence the growth of other phytoplankton species.*

INTRODUCTION

Marine microalgae of the genus *Phaeocystis* are found in all oceans of the world (Kashkin, 1963). The number of species belonging to this genus is not certain, and much of the confusion is due to inaccurate morphological characteristics. Furthermore, while members of this genus are assumed to have complex life histories, not all of the stages have been determined. Morphological investigations have suggested at least nine species (Sournia, 1988), while ribosomal RNA gene sequence studies (Medlin *et al.*, 1994; Zingone *et al.*, 1999) have confirmed only five different species.

Phaeocystis pouchetii (Lagerheim, 1896) is a key component of the phytoplankton spring-bloom in northern and Arctic waters (Eilertsen *et al.*, 1981; Eilertsen and Taasen, 1984; Rey and Loeng, 1985; Weisse *et al.*, 1986; Lancelot *et al.*, 1987; Lancelot *et al.*, 1998) and has been

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described as a coldwater species (Jahnke and Baumann, 1987). Its life cycle is only partly resolved (Rousseau *et al.*, 1994), but it is known to be polymorphic consisting of at least two solitary and one colonial stage. The solitary cell stages have equivalent spherical diameters of 3–4 and 5 μm, respectively, and in both stages the cells have two flagella and one haptonema. The colonial cells are non-motile and encapsulated in a mucilaginous matrix often forming large lobe shaped colonies up to 2 mm in diameter (Chang, 1984). During the culmination phase of a bloom, motile cells are released from the senescent colonies. The ribosomal RNA from *P. pouchetii* along the coast of northern Norway and from the Barents Sea have so far not been sequenced, but transmission electron micrographs indicate that the morphological and physiological characteristics of the cells and the size and the nature of the colonies are similar to that of *P. pouchetii* (Baumann *et al.*, 1994).

The genus *Phaeocystis* belongs to the class Prymnesiophyceae which has frequently been associated with toxin production: cytotoxic properties have been isolated from several species of *Chrysochromulina* and *Prymnesium* (Yasumoto *et al.*, 1990; Aure and Rey, 1992; Stabell *et al.*, 1993). *Phaeocystis pouchetii* has been regarded as a nuisance species because the mucilagous matrix of the colonies can cause clogging of fishing nets and accumulation of foam on beaches (Lancelot, 1995). Anoxia can also occur during dense blooms (Rogers and Lockwood, 1990). Several investigations have indicated that *P. pouchetii* might be responsible for additional adverse effects in the marine environment: As early as 1930 herring was suspected to avoid *P. pouchetii* blooms (Savage, 1930), copepods were later demonstrated to avoid grazing on healthy (young) colonies (Estep *et al.*, 1990), salmon cultivated in sea cages had a pronounced decrease in food intake and growth during the spring bloom of *P. pouchetii* (Eilertsen and Raa, 1995), and water from *P. pouchetii* cultures decreased the survival of cod larvae (Aanesen *et al.*, 1998). Furthermore, organic extracts from *P. pouchetii* were found to be toxic to blowflies (Stabell *et al.*, 1999) and sea urchin embryos (Hansen *et al.*, 2003). The most toxic compound released by *P. pouchetii* has been identified as 2-*trans*-4-*trans*-decadienal (Hansen *et al.*, 2004).

The α,β,γ,∂-unsaturated aldehyde 2-*trans*-4-*trans*-decadienal (DD) was together with two other polyunsaturated aldehydes (PUAs) first identified in the diatoms *Skeletonema costatum*, *Pseudo-nitzschia delicatissima* and *Thalassiosira rotula* (Miralto *et al.*, 1999), and subsequently several related PUAs were found in the same species (Pohnert, 2000; d'Ippolito *et al.*, 2002a; d'Ippolito *et al.*, 2002b; d'Ippolito *et al.*, 2003). The production and release of PUAs by the diatoms are results of decomposition of unsaturated fatty acids in an enzymatic cascade probably induced as a response to mechanical stress. Unsaturated fatty acids liberated from membrane storage sites by phospholipases are converted to lipid hydroperoxides by lipoxygenases, which again are transformed into unsaturated aldehydes by lyases (Pohnert, 2002). The α,β,γ,∂-unsaturated aldehydes have cytotoxic effects on several cell types, e.g. DD inhibits hatching and cell division in crustaceans, echinoderms and polychaetes and cell proliferation in human cells, diatoms and bacteria (see Caldwell *et al.*, 2003). The effect of PUAs produced by diatoms on copepod reproduction has been debated (reviewed by Ianora *et al.*, 2003), and the conclusion seems to be that the PUA producing algae at least have the potential for influencing the survival and growth of grazers, although the exact ecological relevance of this still remains uncertain.

Considerable less attention has been paid to the possibility of chemical interactions between the algae themselves. Allelopathy can be defined as the process in which secondary metabolites produced by algae have negative effects on the growth and development of competing algae (Legrand *et al.*, 2003), and as we know that *P. pouchetii* produce and excrete DD we wanted to study whether this PUA can give *P. pouchetii* a competitive advantage to other species through adverse effects. The present investigation consists of two parts, the first concerns concentration dependency experiments with DD on species naturally co-occurring with *P. pouchetii*, and the second concerns analysis of *P. pouchetii* dominance in field data.

METHOD

Growth and effect experiments

Diatom cultures were germinated from spores contained in sediment samples collected in Austnesfjorden (Fig. 1) and cultivated as monocultures after serial dilution in GF/C-filtered and autoclaved seawater with Gillard's marine water enrichment (Sigma, Aldrich) added to a final concentration of *f*/20. Healthy growing monocultures of the diatoms *S. costatum*, *Thalassiosira antarctica* var. *borealis* and *Chaetoceros socialis* were diluted to appropriate start concentrations (2–3 μg Chl*a* L^{-1}) using the same growth media, thereafter 100 mL portions of the algae suspensions were transferred to 250 mL Erlenmeyer flasks. The DD (Acros Organics, Geel, Belgium) was diluted in 80% methanol, and added to the algae cultures (0.1 mL) to final concentrations of 0.1, 0.5, 1.0 and 5.0 μg mL^{-1}. Flasks containing 0.1% methanol without DD served as controls. The algae were cultivated in a 15:9 h light:dark light regime in a temperature controlled and artificially illuminated room

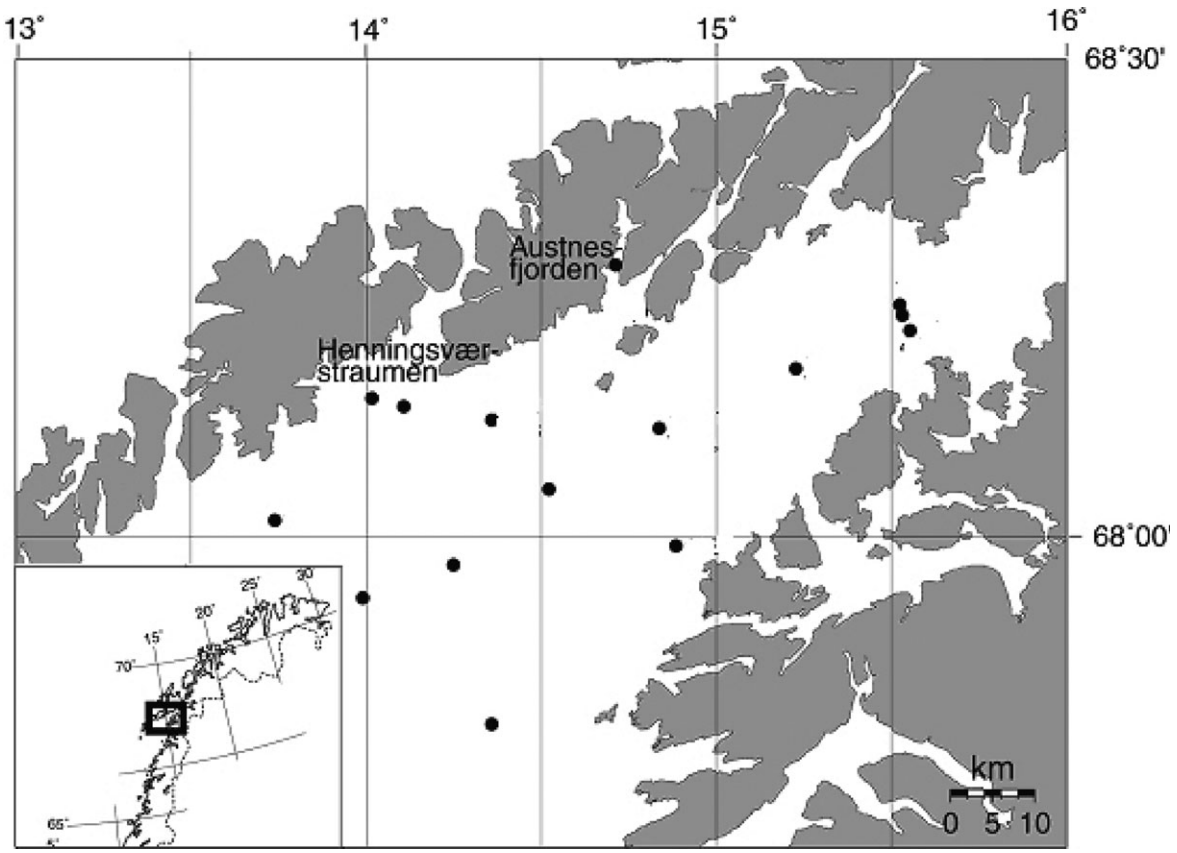

Fig. 1. The locations sampled in Vestfjorden area, Northern Norway March – May 2000 and 2001.

at a scalar irradiance of 50 μmol m^{-2} s^{-1} at 4°C. Experiments have shown that this is above but close to the maximum photosynthesis (P_{max}) irradiance level for these species at this temperature (Gilstad and Sakshaug, 1990). At the start of the experiment, cell concentrations were adjusted according to the size of the cells so that all cultures had biomass concentrations comparable to a mid spring bloom phase, i.e. 2–3 μg Chl*a* L^{-1} (>500 000 cells L^{-1}). The experiment was set up with three replicates for each species, and specific growth rates (μ day^{-1}) were calculated from sub-samples taken at start and after 48 and 96 h. Cells were enumerated live in 4-well Nunclon 2.0 mL sedimenting chambers after >4 h applying the inverted microscope method. Growth rates were slightly lower from 48 to 96 h compared to 0–48 h, and we decided to use specific growth calculated from cell numbers counted after start and 48 h.

Field sampling

Sampling took place during the spring seasons of 2000 and 2001 in Vestfjorden (Lofoten), Northern Norway (Fig. 1) with R/V Jan Mayen (168 ft) or R/V Johan Ruud (100 ft). Single point observations were done along and across Vestfjorden. Diurnal stations (samples collected every fourth hour, Fig. 1; Table I) were sampled in Austnesfjorden, a narrow fjord with sill (30 m) adjacent to Vestfjorden proper and Henningsværstraumen.

Sea temperature (°C), salinity and σ_t (density anomaly) were measured with a Seabird 911plus or General Oceanics MK IIIb CTD.

Currents (N–S, E–W and up–down) were measured with a Vector acoustic doppler velocimeter (NORTEK, Norway) (m s^{-1}) at 5, 10, 25 and 30 m. The measuring period at each depth was 10 min and measurements were only performed during the diurnal stations in Austnesfjorden and Henningsværstraumen. The sampling rate was 8 Hz and the instrument was set to report 1 s means to the logger file.

The modelled vertical eddy diffusivity K_Z (m^2 s^{-1}), also frequently applied as a parameterization of turbulence (Thorpe, 2005), is

$$K_Z = qlS$$

(Blumberg and Mellor, 1987), where S is a function of the Richardson number given by Blumberg and Mellor

Table I: Sampling location, depths, number of species and P. pouchetii fractions

Location/mean depth	Sampling dates	d-pycn. (m)/dσ_t	Chl*a*	Mean number species	Mean *P. pouchetii* fraction
2000					
Vestfjorden/183	23.03	31–0.79	1.68	21 (March 2000)	0.09% (March 2000)
Austnesfjorden/80	21–22.03	9–1.40	4.22		
Henningsværstraumen/50	22–23.03	10–1.20	0.53		
Vestfjorden/214	03–05.04	8–0.44	2.72	40 (April 2000)	0.12% (April 2000)
Austnesfjorden/80	04–05.04	58–0.10	4.07		
Henningsværstraumen/50	05–06.04	50–0.10	4.43		
Vestfjorden/274	11.04	35–0.37	2.95		
Austnesfjorden/85	12–13.04	85–0.60	2.25		
Henningsværstraumen/112	13–14.04	98–0.30	4.13		
Vestfjorden/270	14–18.05	21–3.58	1.48	14 (May 2000)	0.40% (May 2000)
Austnesfjorden/75	24–26.05	10–1.90	1.07		
Henningsværstraumen/65	26–27.05	15–0.60	0.76		
2001					
Vestfjorden/227	19–22.03	130–0.28	2.36	17 (March 2001)	0.09% (March 2001)
Austnesfjorden/74	20–21.03	100–0.00	6.63		
Henningsværstraumen/68	21.03	60–0.00	2.31		
Vestfjorden/247	03–04.04	73–0.19	1.09	31 (April 2001)	0.03% (April 2001)
Austnesfjorden/61	04–05.04	47–0.02	3.60		
Henningsværstraumen/67	05–06.04	60–0.00	1.49		
Vestfjorden/313	08.05	236–0.90	0.17	14 (May 2001)	0.006% (May 2001)
Austnesfjorden/113	11.05	11–0.90	0.56		
Henningsværstraumen/77	09–10.05	57–0.15	0.49		

d-pycn., Pycnocline depth; dσ_t, difference in density between pycnocline depth and surface; Chl*a*, mean Chl*a* concentration 0–50 m in $\mu g\ L^{-1}$.

(1980), l (m) is turbulence length scale and q (m s^{-1}) is turbulence kinetic energy. K_Z was modelled from wind stress and heat flux after input of meteorological parameters sampled onboard the vessels, tides calculated from Gjevik *et al*. (1990), and vertically distributed temperature, salinity and σ_t of the water column (see Hansen and Eilertsen, 1995). Wind stress was calculated from the formula in Gill (1982).

Phytoplankton samples were collected with Niskin 5 L plastic water bottles (General Oceanics Inc.) at fixed depths, i.e. 0, 5, 10, 20, 30, 50 m. Phytoplankton were enumerated and identified to species level by inverted microscopy in 4 well Nunclon 2.0 mL sedimenting chambers onboard the vessels. Proximate volumes of phytoplankton cells were computed as in Smayda (1978). Chlorophyll *a* was measured by collecting the particulates from 10 mL sub-samples from the water bottles onto GF/C filters. Thereafter, extraction (in methanol) and analysis took place according to the method of Holm-Hansen and Riemann (1978) applying a Turner Designs fluorometer.

Further analyses of the data involved linear as well as nonlinear correlation analysis between total biomass (as volume), biomass and fraction of *P. pouchetii* solitary cells, colonies and ghosts (scenesent) colonies, total *P. pouchetii* biomass and number of species, Shannon Wiener diversity index (Hayek and Buzas, 1996), K_Z and current measurements (both were means for the water column above the pycnocline, if pycnocline was absent 30 m was used), dσ_t (increase in σ_t from surface to pycnocline) and pycnocline depth. During the statistical analyses, we applied a break down procedure where we first analysed bulk data and then data from each year, month and cruise.

RESULTS

Growth versus DD-concentration

The *T. antarctica* controls had a specific growth of 0.42 day^{-1}, and growth was decreased in a concentration dependent manner by the presence of DD (Fig. 2, Table II). The growth was moderately impaired at 0.5 $\mu g\ mL^{-1}$ DD (0.12 day^{-1}), and at 1.0 $\mu g\ mL^{-1}$ DD growth was completely blocked. Control cultures of *S. costatum* had higher growth rates compared to *T. antarctica* (0.58 day^{-1}), and the negative effect of the PUA was significantly weaker with a growth rate of 0.16 day^{-1} at 1.0 $\mu g\ mL^{-1}$ DD. *Chaetoceros socialis* controls multiplied fastest (0.78 day^{-1}), and at 0.5 $\mu g\ mL^{-1}$ DD this was reduced to 0.29 day^{-1}, whereas the cells ceased to divide at 1.0 $\mu g\ mL^{-1}$ DD (Fig. 2, Table II).

Data from Vestfjorden

The water columns were more weakly stratified in March–April 2001 than during the same period in 2000 (Table I). The mean phytoplankton biomass

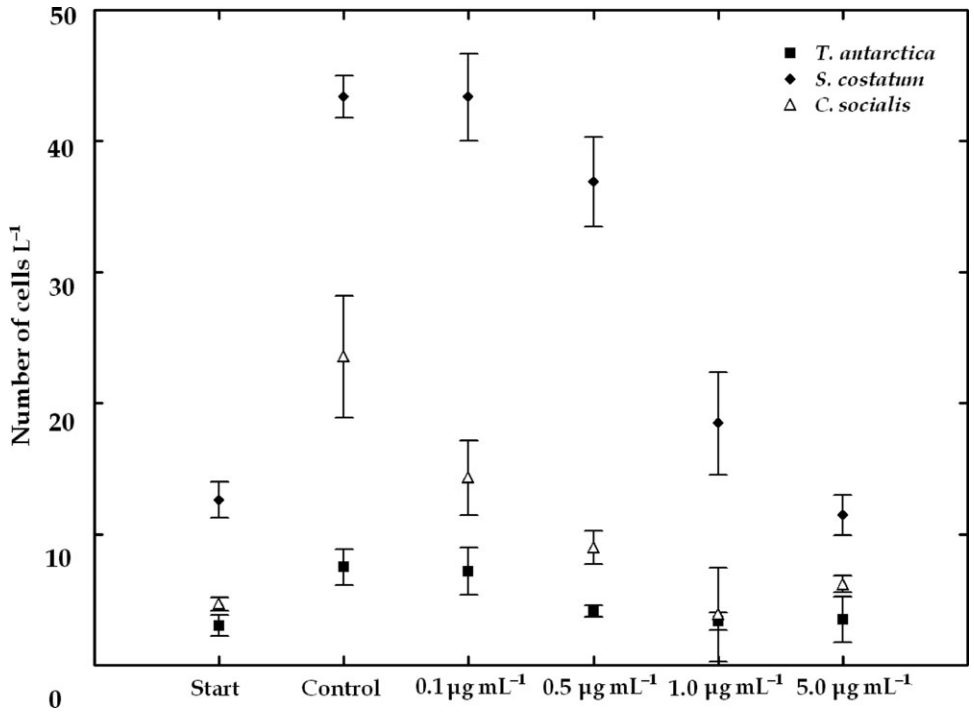

Fig. 2. Cell numbers ($\times 10^6$) from cultivation experiments at start and after 48 h for the various treatments. Numbers are mean of three replicates (± 1 SD, 95%).

peaked in March and April both years, and Chl*a* content and cell numbers varied 0.17–6.63 $\mu g\ L^{-1}$ and 0.6×10^6–18×10^6 cells L^{-1}, respectively. May was characterized by lower concentrations (0.17–1.48 μg Chl*a* L^{-1}), especially in 2001 (Table I). At all stations, the phytoplankton stock consisted of centric diatoms and *P. pouchetii*. The only exceptions were some few stations in the open Vestfjorden in May 2001 where only small unidentified flagellates were found. The nine most important species in terms of biomass (volume integrated over time) for the sampling series were (ranked): *S. costatum; C. socialis; T. nordenskioeldii; P. pouchetii; Fragilariopsis oceanica; T. gravida; C. compressus; Bacteriosira bathyomphala; F. cylindrus.*

The statistical analysis of the data sets showed that it was the linear correlation procedure that yielded the best fits (Table III). It was a significant positive correlation between *P. pouchetii* colony biomass and the diversity, i.e. the diversity increased with *P. pouchetii* biomass. Since the same was the case with total phytoplankton biomass, we also draw the conclusion that in most instances the biomass of *P. pouchetii* increased with increasing total phytoplankton stock. Further, we found no significant correlations between eddy diffusivities (K_Z), currents and diversity (not shown). There was a weak negative correlation between total stock, *P. pouchetii* total biomass and $d\sigma_t$, indicating that the highest biomass occurred when the pycnoclines were weakest. The positive correlation between *P. pouchetii* total biomass and pycnocline depth confirms this (Table III), while negative correlations between month and biomass reflected the fact that the large part of production took place during March and April. The breakdown analyses showed similar trends, except that for some of the stations we observed a positive correlation between K_Z and *P. pouchetii* fraction, and that this occurred at low

Table II: Specific growth rates ($\mu\ day^{-1}$, mean of three replicates) for diatoms incubated at different concentrations of 2-trans-4-trans-decadienal after 48 h

	Control	0.1 $\mu g\ mL^{-1}$	0.5 $\mu g\ mL^{-1}$	1.0 $\mu g\ mL^{-1}$	5.0 $\mu g\ mL^{-1}$
T. antarctica	0.42	0.40	0.12	0.00	0.00
S. costatum	0.58	0.58	0.51	0.16	0.00
C. socialis	0.76	0.53	0.29	0.00	0.10

Table III: Linear correlation analysis (r) performed on data collected from 173 stations during seven cruises performed during the spring seasons 2000 and 2001 in Vestfjorden

	All species	*Phaeocystis pouchetii*							
	Total biomass	Biomass colonies	Biomass solitary	Biomass ghost	Biomass all	Fraction colonies	Fraction solitary	Fraction ghost	Fraction all
Number of species (*n*)	**0.52**	**0.45**	−0.001	0.05	**0.40**	0.01	**−0.23**	−0.02	0.01
Shannon Wiener	**0.24**	**0.22**	−0.002	0.18	**0.20**	0.07	−0.13	0.11	0.07
K_Z	0.08	0.10	−0.004	0.05	0.09	0.05	−0.03	0.09	0.21
$d\sigma_t$	**−0.19**	**−0.18**	**−0.18**	0.05	**−0.26**	**−0.17**	−0.06	0.01	**−0.17**
Pycnocline depth	0.07	0.15	0.13	**−0.2**	**0.21**	**0.17**	0.11	−0.15	**0.17**
Month	**−0.31**	**−0.22**	−0.11	**−0.47**	**−0.25**	**−0.19**	0.07	**−0.29**	**−0.19**

Colonies are solitary *P. pouchetii* cells embedded in mucus, solitary are two types, i.e. with and without flagella while ghosts are empty shells of colonies. Total number of species is *n*, Shannon Wiener is the diversity calculated according to Hayek and Buzas (1996), K_Z is eddy diffusivity and $d\sigma_t$ = difference in density between pycnocline depth and surface. Significant correlations are in bold.

species numbers (Fig. 3). Also there were lower species numbers in May than the two other months.

The mean *P. pouchetii* total fraction (of total stock over time) present in our samples was c. 0.13%, while both biomass and the *P. pouchetii* fraction was overall larger in 2000 than in 2001 (Table I). In terms of occurrence *P. pouchetii* was the only species that was found at all stations. The most important species in terms of cell numbers, *S. costatum* (mean fraction of total stock over time), was the second most important in terms of occurrence (found at 83% of the stations). Further, when *S. costatum* was present *P. pouchetii* was always present in colonial form. The rest of the main species (*C. socialis; T. nordenskioeldii; F. oceanica; T. gravida; C. compressus; Bacteriosira bathyomphala; F. cylindrus)* had occurrences of 54% of total cell number and lower.

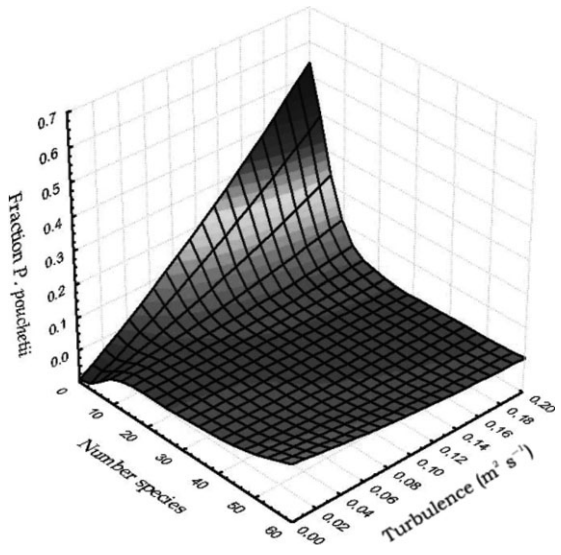

Fig. 3. Fraction of all *Phaeocystis pouchetii* (solitary, colonies, ghosts) computed as volume versus K_Z and number of species.

DISCUSSION

Our experiments with monocultures of three common marine diatoms incubated in different concentrations of DD showed that exponential growth was inhibited in a concentration dependent manner. In a study by Casotti *et al.* (Casotti *et al.*, 2001), the effect of DD on the growth and cell cycle progression of *T. weissflogii* was investigated using flow cytometry. They reported that cells stopped dividing at 0.5 $\mu g\,mL^{-1}$. There seems to be a fairly good agreement between their and our findings with respect to the sensitivity of the tested diatoms towards DD. Unfortunately, we have no data on what levels of DD that can be reached *in situ* during a *P. pouchetii* bloom because the current methods for quantifying PUAs are not sensitive enough (Casotti *et al.*, 2005). It is therefore difficult to conclude whether DD is present in sufficient amounts in the sea in order to act as an allelochemical. Acrylic acid, another potential allelochemical released by *P. pouchetii* (Sieburth, 1960; Guillard and Hellebust, 1971), has been observed at concentrations between 0.037 and 0.051 $\mu g\,mL^{-1}$ during *Phaeocystis* blooms (Yang *et al.*, 1994; Osinga *et al.*, 1996), whereas 230 $\mu g\,mL^{-1}$ is required to reduce the growth of *S. costatum* by 50% (Sverdrup *et al.*, 2001). Normally occurring concentrations of acrylic acid *in situ* are therefore probably far too low to have any significant effect on competing phytoplankton species.

The field samples we collected were typical representatives of spring bloom situations in the Vestfjorden area with respect to species and their relative abundances (Føyn, 1929; Nordli, 1949; Braarud *et al.*, 1958; Braarud

and Nygaard, 1978; Huseby, 2002). The main species making up the bulk of the biomass, e.g. *S. costatum, C. socialis, T. nordenskioeldii, P. pouchetii* and *Fragilariopsis oceanica*, can also be encountered during spring blooms further north along the coast of Norway (Gaarder, 1938; Eilertsen *et al.*, 1981; Hegseth *et al.*, 1995).

The ocean represents a highly dynamic environment, and any compound released into it will be dispersed by small and mesoscale turbulent motion, tending to fill in regions of lower concentration. The modelled eddy diffusivity (K_Z) and current measurements are indirect measures of small scale turbulent motions (Thorpe, 2005). In our data sets K_Z and vertical current were significantly correlated ($R = 0.52$), and both were correlated to wind stress ($r = 0.47$; $r = 0.49$, not shown in table). Modelled eddy diffusivity is also a function of wind regulated cooling of surface water (Q_t) and gradients in the vertical density fields. When modelling of K_Z was repeated for the two uppermost depths where currents were measured (5, 10 m) with heat flux turned off, the correlation between the two turbulence measures improved ($r = 0.64$), and we interpret this as indicative of that the model simulated eddy diffusivity reasonably well. Obtaining a reliable measure of actual degree of turbulence from field measurements is a highly complex task (Foias, 2001). In fact none of the currently available methods are accurate (Thorpe, 2005), but we believe that using modelled K_Z as a measure of potential dispersion of an eventual release of an exotoxin was the best choice for our purpose.

Our statistical analysis did not give any indication that *P. pouchetii* affected the diversity of the phytoplankton stocks in Vestfjorden significantly (Table III). Rather the stock behaved normally, i.e. with the largest diatom and *P. pouchetii* biomass during the exponential phase of the bloom when the pycnoclines were weakest (Tables I and III). Also the diversity of the diatom stocks in Vestfjorden were comparable to situations where the *P. pouchetii* fractions were negligible or zero (Føyn, 1929; Eilertsen *et al.*, 1981). At the stations with a high degree of turbulence, large *P. pouchetii* fractions were associated with low diversity (Fig. 3), i.e. a preference for turbulence (Smayda, 2002). We believe that this was not an allelochemical effect because it would be peculiar if this should occur when dispersion was at its maximum. Rather we believe it reflected that *P. pouchetii* colonies may have some competitive advantages over diatoms since it can have positive buoyancy (Skreslet, 1988). The mean number of species decreased from April to May each year (Table I). We also consider it unlikely that this was a result of a *P. pouchetii* allelochemical since diversity was higher in 2000 compared to 2001. At the same time, both phytoplankton biomass, *P. pouchetii* fractions and water column stability had the highest values in 2000 (Table I). Grazing probably played only a minor role in regulating species abundance since, as is common in northern areas, the copepod stocks are at minimum early in April and nauplii start to be abundant during mid May leading to increased grazing pressure (Båmstedt *et al.*, 1992; Kiorboe, 1998). Simultaneous sampling of zooplankton that took place during our cruises revealed the same trend (Pedersen, 2003). It is common belief that preference for turbulence (Smayda, 2002), competition for light and nutrients (Huisman and Weissing, 1995) and germination strategies of spores (Eilertsen *et al.*, 1995) can influence the co-existence and succession of phytoplankton species (Margalef, 1958). We believe that the reasons for the differences in diversity between the years must therefore be sought here.

When discussing the allelopathic effect of putative toxins or growth regulators in marine systems, it is clear that seasonal variations in the factors controlling mixing of the water column will complicate the interpretation of the between species effects (Tapaswi and Mukhopadhyay, 1999). Since K_Z increases close to boundary layers (here the pycnocline), we interpret K_Z as an indirect measure of dispersion of potential toxins. Increased K_Z should also mean more nutrients added from deeper water, while decreasing K_Z would lead to build up of toxins and lower nutrient levels. We did not measure nutrients regularly during our cruises, but concentrations of nitrate, phosphate and silicon during the May 2001 cruise indicated that nutrient limitation was unlikely since e.g. nitrate was at minimum well above 1 μmol L^{-1} (S. Kristiansen, Tromsø, personal communication). Considering the weak and irregular variations in stratification in our investigation, we tend to believe that if some physical factor was present as regulator, it was mixing and light.

It is notable that our analyses showed that *P. pouchetii* and *S. costatum* dominated the phytoplankton stocks with respect to presence: at 83% of the stations they were both present. The growth rates of *P. pouchetii* may be high at low light levels and low temperatures (Kayser, 1970; Grimm and Weisse, 1985; Eilertsen, 1989), so it cannot be excluded that these species to some degree had an advantage over the other species. However, it cannot in our opinion explain the consistency of the results since strategies favouring high growth rates would also attack the closest competitors (Huisman and Weissing, 2001). This, combined with the fact that both *P. pouchetii* (Hansen *et al.*, 2004) and *S. costatum* (Miralto *et al.*, 1999) have the potential to produce and release DD could indicate that the production of toxins is a trait ensuring some competitive success in shifting environments (Huisman *et al.*, 2001). We can therefore not totally exclude that

during situations with pronounced and shallow pycnoclines, a delayed dilution of toxins could possibly suppress the growth of other species. However, considerable uncertainties connected to the allelopathic function of the PUAs still remains. One is that the PUAs are known to be released by diatoms as a response to mechanical stress (Pohnert, 2000) possibly acting as a defence against grazing (Pohnert *et al.*, 2002). It can therefore not be excluded that the frequent co-existence and presence of these two species in our samples is also the result of grazing deterrence (Estep *et al.*, 1990), even if our quantitative methods did not indicate this. Also our experiments showed that PUA producers are affected by the toxin themselves. Even though *S. costatum* seemed to be able to withstand the negative effects of the PUAs better than the other diatoms, the ecological relevance of this remains an unsolved issue.

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