Effects of small-scale turbulence on lower trophic levels under different nutrient conditions

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Small-scale turbulence affects the pelagic food web and energy flow in marine systems and the impact is related to nutrient conditions and the assemblage of organisms present. We generated five levels of turbulence ($2*10^{-9}$ to $1*10^{-4}$ W kg^{-1}) in land-based mesocosms (volume 2.6 m^3) with and without additional nutrients (31:16:1 Si:N:P μM) to asses the effect of small-scale turbulence on the lower part of the pelagic food web under different nutrient conditions. The ecological influence of nutrients and small-scale turbulence on lower trophic levels was quantified using multivariate statistics (RDA), where nutrients accounted for 31.8% of the observed biological variation, while 7.2% of the variation was explained by small-scale turbulence and its interaction with nutrients. Chlorophyll *a*, primary production rates, bacterial production rates and diatom and dinoflagellate abundance were positively correlated to turbulence, regardless of nutrient conditions. Abundance of autotrophic flagellates, total phytoplankton and bacteria were positively correlated to turbulence only when nutrients were added. Impact of small-scale turbulence was related to nutrient conditions, with implications for oligotrophic and eutrophic situations. The effect on community level was also different compared to single species level. Microbial processes drive biogeochemical cycles, and nutrient-controlled effects of small-scale turbulence on such processes are relevant to foresee altered carbon flow in marine systems.

INTRODUCTION

Laminar and turbulent water movement is generated in the ocean through wind mixing, tides and stratification of water masses and influences food web dynamics at different scales in time and space (Svendsen, 1997). Small-scale turbulence (ε; W kg^{-1}, cm^2 s^{-3}) derived from energy introduced on scales roughly below 10 m may affect planktonic organisms both directly and indirectly. Modified nutrient uptake rates (Lazier and Mann, 1989; Kiørboe, 1993; Karp-Boss *et al.*, 1996) and physiological (Berdalet, 1992), morphological (Zirbel *et al.*, 2000), and behavioural changes (Karp-Boss and Jumars, 1998; Karp-Boss *et al.*, 2000) in phytoplankton are examples of direct effects of small-scale turbulence. Direct effects of natural small-scale turbulence on heterotrophic bacteria are still a controversial topic (Confer and Logan, 1991; Logan and Kirchman, 1991; Malits *et al.*, 2004). Altered habitat, community structure and trophic interactions may, however, influence these organisms indirectly (Bowen *et al.*, 1993; Moeseneder and Herndl, 1995; Peters *et al.*, 1998).

The effect of small-scale turbulence on different plankton groups affects the entire planktonic food web and thus

the direction of carbon flow in the system. Trophic interactions may produce synergetic and antagonistic effects resulting in a total ecological outcome different from theoretical ones based on data from single separate plankton groups. It is therefore important to study the impact of turbulence on planktonic assemblages, and to do so under different nutrient conditions, since small-scale turbulence may affect the community response differently when nutrient conditions vary (Petersen *et al.*, 1998; Arin *et al.*, 2002; Peters *et al.*, 2002). Disentangling the ecological effect of turbulence level and nutrient condition can give new insight in plankton responses to physical forcing under different nutrient regimes, such as conditions dominated by new versus regenerated nutrients (eutrophic versus oligotrophic situations).

The usefulness of mesocosms as a tool for investigating community responses has been thoroughly established (Martínez-Martínez *et al.*, 2006; Riebesell *et al.*, 2007) and the current gradient-based design is an effective tool for inferential studies of ecological processes (Havskum *et al.*, 2003; Thingstad *et al.*, 2008). Land-based mesocosms enable controlled and accurate quantification of the introduced turbulence when compared with bags in the sea (Svensen *et al.*, 2001). In this study, a turbulence gradient was introduced to natural plankton assemblages in unfertilized and nutrient enriched seawater in land-based mesocosms to assess the effects of small-scale turbulence on the planktonic food web under different nutrient conditions.

The main objectives of this work were to (i) investigate if the lower part of the marine pelagic food web was affected by small-scale turbulence and if such an effect (ii) was altered when production was based on regenerated rather than new nutrients.

METHOD

Study site and experimental design

The experiment was conducted between 10 July and 25 July 2001 at the Marine Biological Station of the University of Bergen, Norway. See Egge and Heimdal (Egge and Heimdal, 1994) for a general description of the location.

Two series of five land-based glass fibre tanks (2.6 m^3, 1.5 m diameter, 1.5 m depth, open to the air) were filled with screened (180 μm Nytex mesh) seawater from 2 to 3 m depth on July 10 (Fig. 1). The mesocosms were situated in larger plastic tanks, where continuous water flow with fjord water dampened temperature fluctuations. One series of mesocosms received an initial addition of nutrients, while another series was held unfertilized

(Table I), simulating ecological situations based on new and regenerated nutrients, respectively (Fig. 2). The nutrient addition of silicate (Na$_2$SiO$_3$), nitrate (NaNO$_3$) and phosphate (KH$_2$PO$_4$) was in accordance with the Redfield ratio, though a surplus of Si was added to avoid Si limitation for diatoms (Si:N:P 32:16:1 μM). Turbulence grids were made of two Plexiglas grids (10 cm opening, 5 cm grid width) held in a Teflon-covered stainless steel frame and placed at 1 m depth and with a vertical stroke of 40 cm. By regulating the vertical movement of the grid (speed, frequency and stroke), a turbulence gradient with four turbulence levels was established. The fifth tank of each series was not influenced by artificial turbulence (Table I). The methods by Stiansen and Sundby (Stiansen and Sundby, 2001) were applied to estimate turbulent kinetic energy dissipation rates (ε; W kg^{-1}, cm^2 s^{-3}) from velocity measurements performed with an acoustic Doppler flow meter (NDV field, Nortek AS). This method is developed specifically to calculate dissipation rates in a zero mean flow environment, such as mesocosms or laboratory tanks. It has earlier been used with success in similar systems (Nerheim *et al.*, 2002; Utne-Palm and Stiansen, 2002; Guadayol *et al.*, 2009). Bulk average *in situ* energy dissipation rates were of 1–3*10^{-7}, 5–8*10^{-6}, 1*10^{-5} and 1*10^{-4} W kg^{-1}. Energy dissipation rates in the still tanks, caused by thermal convection and salinity gradients only, were measured to be 2*10^{-9} W kg^{-1}. The application of a two-grid system in each tank minimized heterogeneity by covering as much vertical distance as possible. Turbulence in the mesocosms was nearly isotropic, based upon the spectral density found (−5/3 slopes) and the bulk homogeneity in turbulent kinetic ε (Beauvais *et al.*, 2006). The size of the tanks (i.e. ∼O (1 m)) was large enough to ensure that the largest vortices in the turbulent cascade were well above the relevant turbulent scale for the plankton encounters in the tank (i.e. ∼O (10 cm)) (Sundby, 1997). The measured dissipation rates are in the range of turbulence levels found in the world oceans (MacKenzie and Legget, 1993; Simpson *et al.*, 1996), notably in coastal areas (Kiørboe and Saiz, 1995).

To ensure homogenous light conditions in all mesocosms, the glass fibre tanks were made of non-permeable material, only allowing light penetration from above. In addition, turbulence grids were also included in the still tanks to assure equal light conditions along the turbulence gradient.

Physical, chemical and biological *in situ* measurements

Surface irradiance (PAR) was measured with a Li-190SA Quantum Sensor and recorded by a Li-Cor
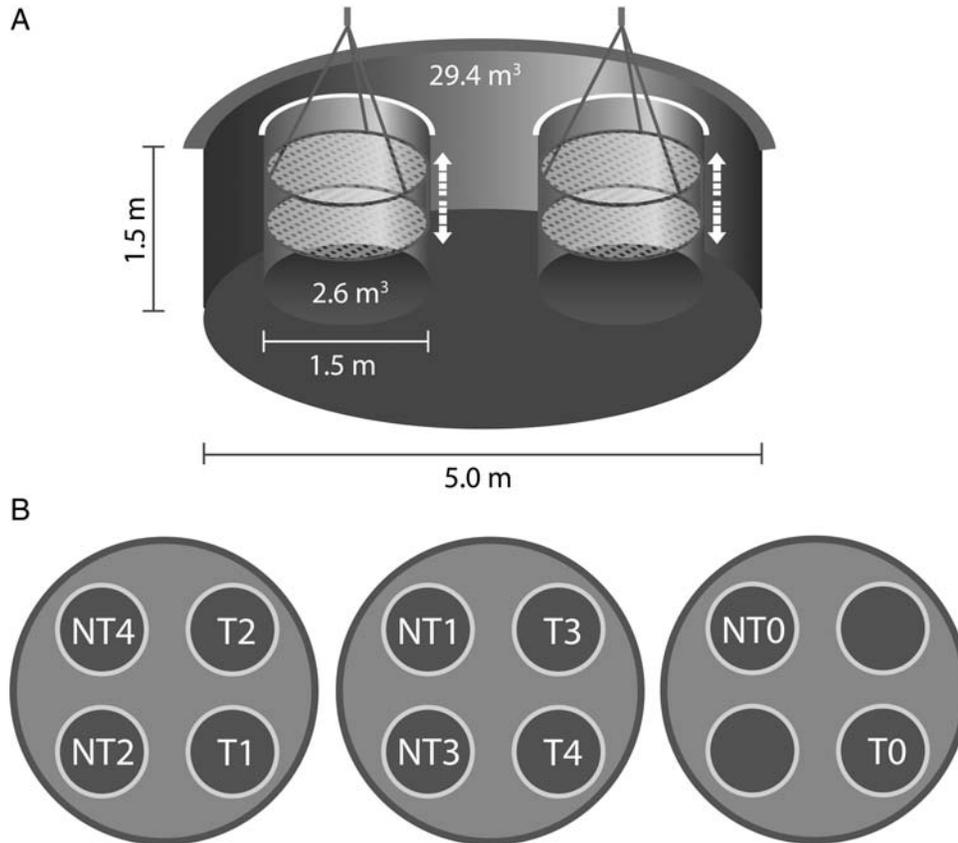
Fig. 1. (**A**) Schematic view of land-based mesocosm system with mesocosms, outer tanks and turbulence generators and (**B**) relative positions of the mesocosms during the NTAP experiment 2001.

Table I: Terminology and in situ dissipation rates (ε; W kg^{-1}) for mesocosms with no additional nutrients (T-gradient/low nutrient) and initial nutrient addition (NT-gradient; Si:N:P 32:16:1/ high nutrient) along a turbulence gradient used in the mesocosm experiment in Bergen July 2001

Dissipation Rate ε (W kg^{-1}) T/NT	Low nutrient	High nutrient
2×10^{-9}	T0	NT0
$3 \times 10^{-7}/1 \times 10^{-7}$	T1	NT1
$5 \times 10^{-6}/8 \times 10^{-6}$	T2	NT2
$1 \times 10^{-5}/1 \times 10^{-5}$	T3	NT3
$1 \times 10^{-4}/1 \times 10^{-4}$	T4	NT4

Li-1000 Data Logger. Salinity and temperature (°C) were measured every other day between 09:00 and 10:00 h with a STD/CTD, model SD 204 (SAIV A/S Environmental Sensors & Systems). Analyses of silicate and phosphate were conducted on fresh samples (Koroleff, 1983; Valderrama, 1995), using a Shimadzu UV-160 Spectrophotometer. Nitrate was analysed on a Skalar autoanalyzer from samples preserved with chloroform (Hagebø and Rey, 1984), immediately after the experiment.

Integrated water samples from the entire water column were collected between 08:30 and 09:00 h every other day using a Plexiglas tube (5 cm diameter, 3 L volume). Diatom samples (10 mL) preserved with pseudolugol (lugol-glutaraldehyde solution—35‰ w/w) (Jensen, 1998) were counted using the method of Utermöhl (Utermöhl, 1931). Dinoflagellates were enumerated and identified from water samples on 11 July, 16 July, 20 July and 25 July and interpolated for the remaining sampling days. For enumeration of dinoflagellate species >20 μm, samples were fixed with Lugol's solution (final concentration 10%) and the Utermöhl technique was applied (Utermöhl, 1958). Dinoflagellate species <20 μm and autotrophic flagellate samples were fixed with glutaraldehyde (final concentration 1%) before filtering them onto 0.8 μm black polycarbonate filters and staining them with DAPI (Porter and Feig, 1980) at 5 μg L^{-1}. The filters were mounted on slides and subsequently frozen at -20°C
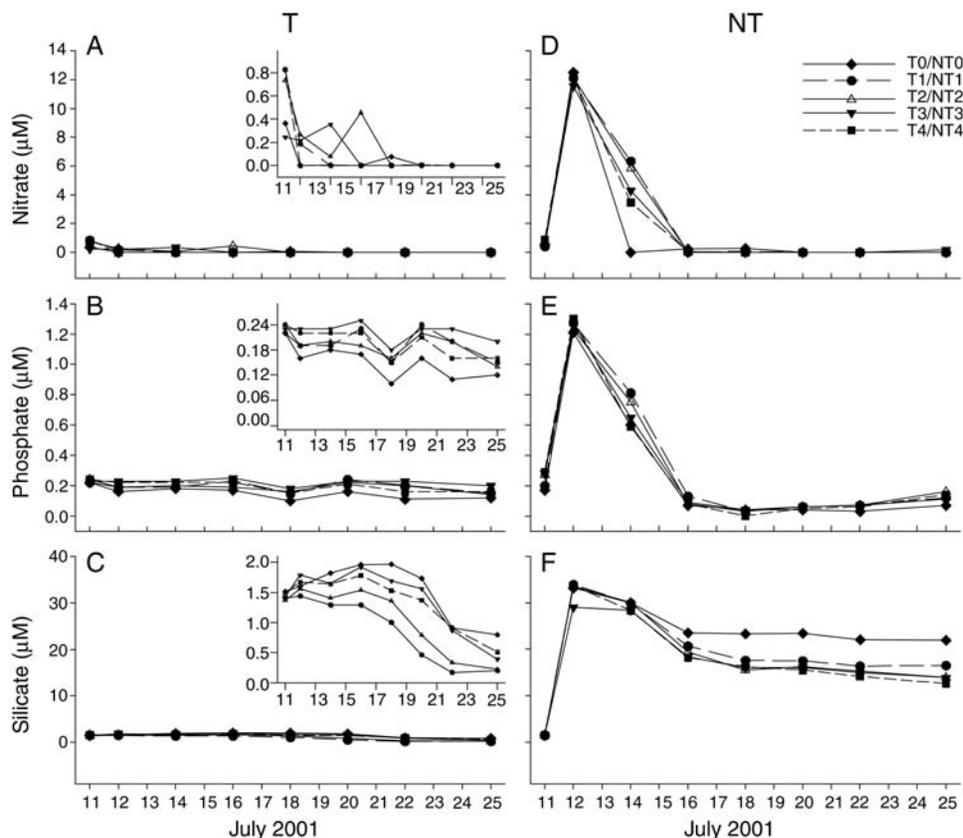
Fig. 2. Concentration (μM) of (**A** and **D**) nitrate, (**B** and **E**) phosphate and (**C** and **F**) silicate in unfertilized mesocosms (T0–T4) and in enriched mesocosms (one initial addition of 32:16:1 Si:N:P μM; NT0–NT4) along a turbulence gradient during the NTAP experiment 2001.

to preserve the chlorophyll autofluorescence (Porter and Feig, 1980; Bloem *et al.*, 1986; Sanders *et al.*, 1989), before being counted in a Nikon Labophot epifluorescence microscope in blue light at ×1250 magnification. For the purpose of statistical analysis, abundance for the three algal groups counted (diatoms, flagellates and dinoflagellates) were implemented in the data set both as separate groups and as total phytoplankton abundance (10^6 total number of cells L^{-1}).

Abundance of heterotrophic bacteria was determined by flow cytometry (FCM). All FCM analyses were performed with a FACSCalibur flow cytometer (Becton Dickinson) equipped with an air-cooled laser providing 15 mW at 488 nm equipped with standard filter set-up. Enumeration of bacteria was performed on samples fixed with glutaraldehyde for 60 s at an event rate between 100 and 1000 s^{-1}. Each sample was diluted 50- to 500-fold before they were stained with SYBR Green I. Flow cytometer instrumentation and the remaining methodology followed the recommendations of Marie *et al.* (Marie *et al.*, 1999). For more details, see Larsen *et al.* (Larsen *et al.*, 2001).

Chlorophyll *a* (chl *a*) was measured fluorometrically (Parsons *et al.*, 1984). Water samples of 20 mL were filtered through nitrocellulose filters (0.22 μm pore size) and chl *a* extracted for 24 h in 7 mL of 90% acetone. The fluorescence of the extract was measured with a Turner Design Fluorometer (Model 10-AU), calibrated with pure chl *a* (Sigma).

Primary production was measured using the ^{14}C method (Steeman Nielsen, 1952; Gargas, 1975). Water samples stained with 4 μCi were incubated in NUNC Easyflasks (76 mL) and attached to turbulence generators in the mesocosms for ~150 min between 11:00 and 14:00 h. The samples were thus not incubated under *in situ* turbulence, but the temperature and oscillating light conditions were as for suspended cells in the mesocosms. The measured primary production rates reflect the phytoplankton response to the recent history of nutrient and turbulence conditions in each individual mesocosm. After incubation, samples were filtered onto Sartorius membrane filters (0.45 μm) and frozen (−20°C). The samples were later counted in a Packard Tri Carb Liquid Scintillation Analyser, model 1900 A,

after fuming with HCl. Total CO_2 was calculated through alkalinity measurements (Parsons *et al.*, 1984).

Bacterial production was measured by incorporation of tritiated leucine (60 nM final concentration) in bacterial protein synthesis (Kirchman *et al.*, 1985), as modified by Smith and Azam (Smith and Azam, 1992). The samples were incubated in still and dark conditions at *in situ* temperatures for 60 min, when the production was stopped by adding 100% trichloricaceticacid (TCA). Samples were stored at 4°C prior to counting in a Packard Tri Carb Liquid Scintillation Analyser, model 1900 A. The bacterial uptake of leucine was converted to bacterial carbon production (BCP) (Simon and Azam, 1989). While bacterial production measurements were not incubated *in situ*, they still reflect the recent history of nutrient and turbulence conditions in each individual mesocosm.

Data analysis

The multidimensional nature of the collected data, with several response variables (chl *a*, PP, etc.) being measured for the autotrophic and heterotrophic components of the plankton community in each experimental unit, and the turbulence gradient generated by treatment design, prompted the application of multivariate analysis. Multivariate ordination methods are an efficient tool for the analysis of ecological gradients (Legendre and Legendre, 1998), exploiting the correlations between response variables, a valuable feature for the present study which aimed at an integrated analysis of the plankton community response to small-scale turbulence. Ordination methods (Legendre and Legendre, 1998) were used to describe the variation in response variables (Principal Component Analysis, PCA) and model their relationships with the manipulated factors (Redundancy Analysis, RDA). PCA has been successfully applied in earlier investigations of turbulence effects on phytoplankton (Estrada *et al.*, 1987; Estrada *et al.*, 1988).

Further, RDA allows partitioning of the influence of different environmental factors on the total variation in the plankton community response, thereby allowing to tease apart the relative effects of small-scale turbulence and nutrient conditions (Legendre and Legendre, 1998). Several models specifying alternative relations between response variables and manipulated factors (including their quadratic and interaction terms) were estimated using the statistical software CANOCO (ter Braak and Šmilauer, 2002) and their performance was compared. The alternative models included factors associated with (i) nutrient concentration, (ii) turbulence level (both linear and quadratic term) and (iii) turbulence level (both linear and quadratic term) and its interaction with nutrient treatment. Model selection based on goodness of fit criteria (selecting model accounting for highest variation in response variables) allowed us to assess the shape and structure of the relationships between plankton responses and small-scale turbulence. The response variables were log transformed, centred and standardized to facilitate comparison and to meet the underlying assumptions of RDA. The dinoflagellate abundance, comprising original and interpolated values, was included as a passive variable to avoid influence on the overall analysis. When analysing the influence of small-scale turbulence, the nutrient factor was dummy coded and introduced as covariate to correct for differences in mean values between nutrient treatment groups and to remove its effect on biological variation. Model results were reproduced in ordination biplots summarizing the main trends in the data. The biplot displays response and explanatory variables as vectors (arrows point in the direction of increasing variable values) in a reduced ordination space (e.g. two dimensions). Correlations between variables are shown by the angle between arrows (an angle of less than 90° between two arrows of interest implies positive correlation), whereas the length of an arrow depicts the strength of association between a variable and the ordination axes shown in the biplot. Models were tested by permutation (Monte Carlo test, with 500 permutations) (Legendre and Legendre, 1998), to check whether the response variables were significantly correlated with turbulence and nutrient regimes.

RESULTS

The temporal dynamics of microbial abundance and production varied greatly between unfertilized and enriched mesocosms (Fig. 3). In the unfertilized mesocosms (T-gradient), phytoplankton abundance (Fig. 3A) and primary production rates (Fig. 3B) peaked under initial nutrient conditions with a second increase in primary production towards the end of the experiment. The nutrients added to the NT-gradient caused classic phytoplankton blooms to develop with peaks in phytoplankton abundance and primary production rates (Fig. 3E and F) between 14 July and 16 July with a culmination of both on 18 July. Maximum phytoplankton abundance and primary production rates based on numbers used in Fig. 3 were, respectively, 2.7–8.6 times and 7.2–11.2 times higher in the NT- than in the T-gradient.

Total phytoplankton abundance, primary production rates and bacterial production rates in unfertilized
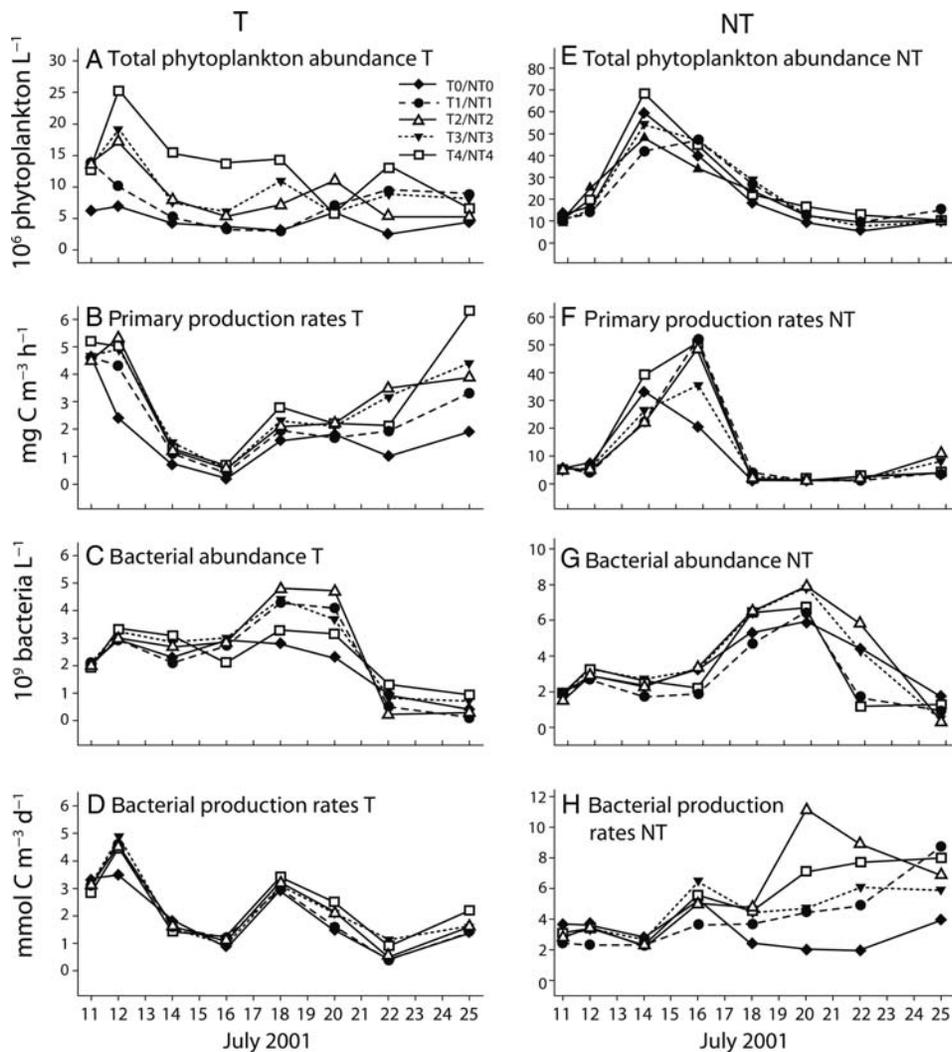
Fig. 3. Temporal trends in (**A** and **E**) total phytoplankton abundance (10^6 cells L^{-1}), (**B** and **F**) primary production rates (mg C m^{-3} h^{-1}), (**C** and **G**) total bacterial abundance (10^9 cells L^{-1}) and (**D** and **H**) bacterial production rates (mmol C m^{-3} day^{-1}) in unfertilized mesocosms (T0–T4) and in enriched mesocosms (NT0–NT4) along a turbulence gradient during the NTAP experiment 2001. Note the different scales.

mesocosms all displayed an initial peak (Fig. 3A, B and D), while bacterial abundance was low at the beginning of the experiment (Fig. 3C). Total phytoplankton abundance in general experienced a steady decrease throughout the experiment. The trend appeared different for primary production rates, bacterial abundance and bacterial production rates, which all showed a second peak in abundance and production rates midway in the experimental period. In addition, both primary and bacterial production rates increased in the final stage of the experiment. In the enriched mesocosms, the bacterial abundance and production rates increased substantially after 18 July, when the phytoplankton bloom culminated (Fig. 3G and H). The difference in bacterial production rates between

turbulence levels increased substantially in the same period. Maximal bacterial abundance and production rates based on numbers used in Fig. 3 were, respectively, 1.5–2.0 times and 1.3–2.5 times higher in the NT-gradient when compared with the T-gradient.

The statistical analysis revealed that nutrient treatment explained 31.8% of the total variation in the dependent variables (Monte Carlo test, $P = 0.002$). Small-scale turbulence alone accounted for 5.5% of the overall variation (Monte Carlo test, $P = 0.06$). When including the interaction between small-scale turbulence and nutrients, the explanatory power, however, increased from 5.5 to 7.2% presented in the RDA model (Monte Carlo test, $P = 0.08$; Fig. 4). When investigating the effect of small-scale turbulence and its
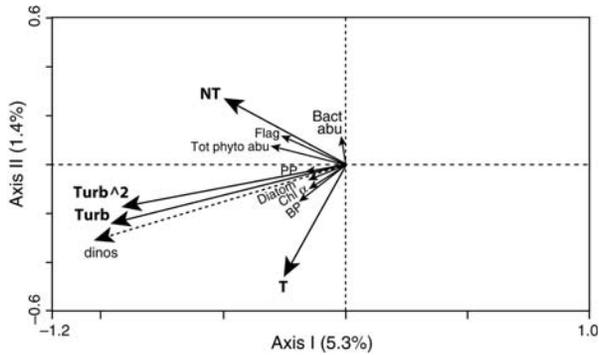
Fig. 4. Biplot of ordination model (RDA) results showing response variables relations to small-scale turbulence (Turb, linear term; Turb^2, quadratic term) and its interaction with nutrient treatment (T, unfertilized mesocosm; NT, enriched mesocosm – see Method section for biplot interpretation). The model shows a positive relationship between the response variables and turbulence (along first ordination axis), with the response to turbulence of different variables being contingent on nutrient level. The interpolated dinoflagellates data set was introduced as a passive variable.

interaction with nutrients, the biological response variables fell into different categories (Fig. 4). Chlorophyll *a* (chl *a*), primary production rates, diatom abundance and bacterial production rates were all positively correlated to turbulence (both the linear and quadratic term) independent of nutrient conditions. The direction and length of the arrow associated with the passive variable of dinoflagellates indicates that this group was strongly positively correlated to turbulence (both linear and quadratic term) independent of nutrient level. The autotrophic flagellates and the total phytoplankton abundance (as a result of the high abundance of autotrophic flagellates) showed a stronger positive correlation to turbulence when nutrients were added to the system, whereas bacterial abundance was correlated to turbulence only under nutrient enrichment. Since bacterial production was positively correlated to turbulence in general and slightly stronger under low nutrient conditions, bacterial abundance and production were negatively correlated.

DISCUSSION

A gradient of increasing levels of dissipation rates is useful when attempting to investigate shape and character of potential relationships between small-scale turbulence, nutrient conditions and planktonic organisms. Our design has proven adequate in studies measuring several biological parameters from multiple experimental units (mesocosms) along an ecological gradient over time (Havskum *et al.*, 2003; Thingstad *et al.*, 2008). Combined with multivariate statistical analysis, this

experimental set-up enabled us to characterize the aggregated response of the plankton community (Legendre and Legendre, 1998). Our application of multivariate statistical analysis facilitated the suppression of nutrient impact by dummy coding it and thus quantifying the statistical fraction of variation explained by small-scale turbulence under different nutrient conditions. This approach allowed us to present quantitative estimates of the effect of nutrient condition and small-scale turbulence on the lower part of the pelagic food web for the first time, to our knowledge.

We introduced a turbulence gradient to natural plankton assemblages in unfertilized (T-gradient) and nutrient enriched (NT-gradient) seawater to assess the effects of small-scale turbulence on the planktonic food web under different nutrient conditions. The plankton community in the NT-gradient was provided with an initial nutrient addition and resembled natural communities dominated by new production, like upwelling areas or spring bloom situations. Mesocosms that received no nutrients (T-gradient) can be compared with oligotrophic waters or summer stratification situations where regenerated production dominates. Not surprisingly the most profound effects, causing different development in abundance and production rates of both phyto- and bacterioplankton between the two gradients, were caused by this fundamental difference in nutrient conditions. Multivariate statistical analysis, however, showed that small-scale turbulence alone accounted for 5.5% of the total variation in the dependent variables (chlorophyll *a*, primary production rates, bacterial production rates and abundance of heterotrophic bacteria, total phytoplankton, autotrophic flagellates, autotrophic dinoflagellates and diatoms). When including the interaction between small-scale turbulence and nutrients, the explanatory power increased from 5.5 to 7.2%. Our analyses thus showed that in the current experiment, 7.2% of the total variance in response variables was explained by turbulence-related effects (turbulence only + turbulence-nutrient interactions). The effect of small-scale turbulence on the lower part of the pelagic food web should thus not be overlooked.

Diatoms and dinoflagellates positively correlated with turbulence regardless of nutrient conditions

The biological response variables chlorophyll *a* (chl *a*), primary production rates, bacterial production rates and abundance of diatoms and dinoflagellates were all positively correlated to turbulence (both the linear and quadratic term) independent of nutrient conditions.

A general positive correlation between small-scale turbulence, primary production rates and abundance of diatoms and dinoflagellates are all surprising observations. Enhanced small-scale turbulence may increase nutrient fluxes towards larger phytoplankton cells (Lazier and Mann, 1989; Mann and Lazier, 1991; Karp-Boss et al., 1996) like diatoms if these are diffusion limited (Pasciak and Gavis, 1974; Gavis, 1976; Savidge, 1981). In the current experiment, small-scale turbulence seemed to affect diatoms and primary production rates regardless of nutrient conditions. Arin et al. (Arin et al., 2002) also found that turbulence increased the proportion of diatoms to the total phytoplankton biomass in all nutrient treatments.

Our results challenge the theoretical assumption regarding direct effect of small-scale turbulence and minimum cell size. According to taxonomic data from the current experiment, *Chaetoceros danicus* was the most abundant species in unfertilized mesocosms, while *Skeletonema costatum* and *Thalassiosira* sp. dominated the diatom community in the enriched treatment (Beauvais et al., 2006). Size measurements showed that the individual cells of all three species $<60\,\mu$m (A. Jacobsen, unpublished data), which is below the smallest threshold size for assumed effects of small-scale turbulence on nutrient fluxes to planktonic cells (Karp-Boss et al., 1996). Formation of chains could alter how individual diatom cells are affected by small-scale turbulence and enhanced chain length associated with turbulence has been reported earlier (Arin et al., 2002). The relationship between cell shape, potential chain formation, nutrient uptake and turbulence is, however, a complex one.

The work of Pahlow et al. (Pahlow et al., 1997) concludes that single cells and simple short chains of diatoms are favourable under low nutrient conditions and weaker turbulence associated with post-bloom scenarios. According to the literature, *C. danicus* appears as solitary cells or builds short chains, while *S. costatum* and most *Thalassiosira* species are known to build longer chains with gaps between individual cells. Overall, chain formation decreases diffusive nutrient supply, making bloom situations with high nutrient concentrations and stronger turbulence less disadvantageous for chain forming species. However, gaps between cells in chains, like the ones found for both *S. costatum* and the *Thalassiosira* species present, could enhance the diffusive nutrient supply to individual cells due to reduced biomass per unit of chain length. Spaces between the chain's cells could therefore give an advantage even larger than the one experienced by solitary cells. Dominating species in both nutrient treatments in our experiment thus seemed adapted to enhancement of nutrient supply under the different nutrient and turbulence conditions. It is tempting to speculate that bottom-up processes related to nutrient fluxes could have been positively affected by small-scale turbulence in both nutrient scenarios, creating the overall positive correlation between diatoms and turbulence. These observations challenge the assumption that small-scale turbulence only has potential to increase nutrient fluxes at low or intermediate nutrient concentrations and could be due to resistant diffusion limitation even under nutrient fertilization.

The surprisingly strong positive correlation between turbulence and autotrophic dinoflagellates in our experiment also calls for alternative explanations since dinoflagellates are known to thrive under calm conditions, supposedly due to general high sensitivity to turbulent motion (Thomas and Gibson, 1990; Estrada and Berdalet, 1997; Zirbel et al., 2000). Our results seem to support a more nuanced notion, where the effect of small-scale turbulence can affect different groups, species or even individual cells within the same taxonomic group differently (Berdalet and Estrada, 2005; Berdalet et al., 2007). Results from experimental work have proposed that the effect of small-scale turbulence on dinoflagellates could be species-specific (Sullivan and Swift, 2003; Berdalet et al., 2007) where the impact is related to cell size and morphology (Latz et al., 2004) or the combination of environmental factors and physiological state of cells present (Juhl et al., 2000; Havskum and Hansen, 2006). Our work suggests that this view should also be applied for other taxonomic or functional groups as well, such as diatoms.

Ecological effects of small-scale turbulence act differently under new versus regenerated production

Findings in our experiment imply that the effect small-scale turbulence exerts on some planktonic groups differs when production is based on regenerated rather than new nutrients. According to our data and multivariate statistical analysis, both autotrophic flagellate and bacterial abundance were more strongly correlated to enhanced turbulence under high than low nutrient concentrations. Since both autotrophic flagellates ($<20\,\mu$m) and bacteria ($<2\,\mu$m) are regarded as too small ($<60\,\mu$m) to be affected directly by small-scale turbulence (Lazier and Mann, 1989; Mann and Lazier, 1991; Karp-Boss et al., 1996), these observations probably are the result of bacteria being affected through turbulence-altered trophic interactions. Previous experiments have indeed shown that small-scale turbulence has a positive effect on bacterial abundance and our results are in concert with these findings (Peters et al.,

1998; Peters *et al.*, 2002). One suggested explanatory factor is that turbulence changes the encounter rates between heterotrophic microplankton and more preferred prey (picoplankton and nanoflagellates), thus releasing bacteria from grazing pressure (Shimeta *et al.*, 1995; Peters *et al.*, 2002). In addition, Malits *et al.* reported that bacterial abundance also can be more directly affected through increased availability of large dissolved molecules and colloids (Malits *et al.*, 2004), but such processes are not possible to comment upon on the basis of the current investigation.

Results from our experiment did, however, show that the production of transparent exopolymeric particles (TEP) increased along the turbulence gradient, especially in the enriched mesocosms (Beauvais *et al.*, 2006). This could facilitate favourable conditions for bacteria and provide a plausible explanation for the positive bacteria−turbulence relationship found in fertilized mesocosms. Nutrient enrichment increases the ecological effect of small-scale turbulence through facilitating more biomass for the physical forcing to act on (Petersen *et al.*, 1998; Peters *et al.*, 2002; Arin *et al.*, 2002) and the exclusive correlation between bacterial abundance and small-scale turbulence in enriched mesocosms shown here could be explained by such processes. Shifts in predation pressure from bacteria to pico- and nanoplankton should induce a parallel reduction in abundance of the latter organisms. Such ecological dynamics are, however, yet to be shown and our results add to the controversy since autotrophic flagellates in the current experiment are positively correlated to small-scale turbulence under higher nutrient concentrations.

The effect of small-scale turbulence on bacterial production rates

From the current experimental set-up and resolution of bacteria-related parameters, it is difficult to explain the relationship between bacterial production rates and small-scale turbulence in our experiment. According to our multivariate statistical analysis, it appears that bacterial production rates were positively correlated to small-scale turbulence in general and slightly stronger under low nutrient conditions. Diatom abundance and primary production rates were positively correlated to small-scale turbulence regardless of nutrient conditions, and phytoplankton−bacteria interactions could constitute the basis for the pattern of bacterial production rates. Microzones surrounding phytoplankton cells, the phycosphere, have been suggested as an important source of substrate for bacteria (Bell and Mitchell, 1972; Mitchell *et al.*, 1985). This hypothesis is, however, controversial, together with the potential importance of

bacterial clustering around phytoplankton cells (Bowen *et al.*, 1993).

The multivariate statistical modelling also suggests that bacterial production rates potentially could be more strongly correlated to small-scale turbulence at low nutrient concentrations. If this is the case, the result could give support to reports on turbulence-induced increase in uptake of certain low-molecular-weight dissolved organics like leucine in oligotrophic environments (Logan and Kirchman, 1991). This effect is, however, thought to be more pronounced for particle-attached than free-living bacteria and we do not have data on the composition of bacteria from our experiment to test this assumption. Overall, speculations concerning turbulence induced changes in substrate access add to the controversy on whether or not bacteria can be directly affected by small-scale turbulence (Confer and Logan, 1991; Bowen *et al.*, 1993; Moeseneder and Herndl, 1995) but cannot be explained from the current experiment.

Small-scale turbulence connecting nutrients, lower trophic levels and biogeochemical processes?

Marine microorganisms have the ability to respond to altered turbulence conditions through for instance reversible morphological changes optimizing the manoeuvring capacity of the cell (Zirbel *et al.*, 2000) or simply by modifying the viscosity of the surrounding water masses, altering the energy dissipation rates experienced (Jenkinson, 1986; Jenkinson and Biddanda, 1995). Such findings, in concert with unexpected findings related to phyto- and bacterioplankton in our experiment, suggest that the effect of small-scale turbulence should be regarded as species-specific as for other environmental factors. The observed discrepancy between turbulence effects in bacterial production rates and abundance even puts forward the possibility of heterogeneous responses in different ecological processes within the same functional group.

It is also tempting to speculate that some of our findings are the result of possible effects on grazers (Rothschild and Osborn, 1988), which cascade downwards in the planktonic food web creating synergetic and/or antagonistic effects on different phyto- and bacterioplankton groups. Further, altered trophic interaction, as potential shifts in predation pressure, symbiotic relationships and composition of the nutrient pool, might influence biological features (e.g. primary production rates) traditionally considered as evidence of more direct effects of small-scale turbulence. The segregation between direct and indirect effects of small-scale

turbulence may thus turn out to be a sub-optimal tool for understanding the ecological impacts of turbulence level on the planktonic community.

The observation that bacterial production rates and bacterial abundance are differently affected by small-scale turbulence related to nutrient conditions in our experiment shows how altered processes at lower trophic levels potentially affect large-scale biogeochemical processes. Bacterial production rates are bottom-up regulated through substrate limitation, while bacterial abundance is top-down regulated by predation. A nearly opposite response to turbulence may therefore indicate different ecological regulations of bacteria in environments dominated by new versus regenerated nutrients. Our findings indicate that the effect of turbulence level on bacterial substrate access or nutrient assimilation differs less under different nutrient conditions than top-down regulation of bacteria through predation, which is reduced under eutrophic nutrient conditions. If these explanatory attempts hold, our results could imply that small-scale turbulence both controls the uptake of organic carbon as well as direction of carbon flow in the bacteria-based compartment of the lower pelagic food web dependent on the present nutrient conditions.

Processes taking place at the lower trophic levels in the pelagic food chain thus have implications for biogeochemical cycles through strength and direction of the carbon flow. Transparent exopolymeric particles (TEP) production, aggregation and formation of marine snow represent further regulatory factors affecting biogeochemical processes. Earlier work has related physical coagulation processes, like turbulence, to the upper limitation of accumulation of phytoplankton blooms, thus having impact on aggregate formation and sedimentation of phytoplankton cells (Jackson, 1990; Kiørboe et al., 1990). Results from the current experiment showed a positive correlation between enhanced TEP production and turbulence level, especially under high nutrient conditions (Beauvais et al., 2006). At the same time, our multivariate statistical analysis showed that while abundance of diatoms and dinoflagellates, chl a, primary and bacterial production rates all were positively correlated to small-scale turbulence regardless of nutrient conditions, the abundance of autotrophic flagellates and bacteria were more susceptible to turbulence effects under high nutrient concentrations. These findings suggest that to understand the implications of altered turbulence and nutrient conditions for coagulation processes and vertical export of biological matter related to climate change, further effort must be invested in enhanced resolution concerning the effect of small-scale turbulence on marine plankton in oligotrophic and eutrophic water masses. Species-specific

responses, heterogeneous responses in different ecological features within the same functional groups (e.g. bacterial abundance and bacterial production rates) and altered trophic interactions are all aspects complicating the matter which should be investigated in more detail.

CONCLUSIONS

One effect of the already experienced and the further foreseen climate change is altered wind conditions. This in turn will lead to changes in the small-scale turbulence that the plankton community experiences. Microbial processes drive biogeochemical cycles, and nutrient-controlled effects of small-scale turbulence on such processes are thus relevant to foresee altered carbon flow in marine systems. In concert with earlier investigations, our experiment and multivariate analysis have shown that the lower part of the marine pelagic food web was affected by small-scale turbulence. Further, we have demonstrated that the ecological impact of small-scale turbulence may differ when production is based on regenerated rather than new nutrients. Altered turbulence conditions may thus have different ecological impact in oligotrophic oceanic regions such as the Mediterranean or the open ocean when compared with eutrophic ones, as for instance the Norwegian Sea and coastal areas. Our results also revealed that differences in small-scale turbulence can give surprising effects when it impacts the whole planktonic community as compared to a single species? Puzzling results for phyto- and bacterioplankton concerning species-specific effects, planktonic threshold cell size and controlling ecological factors related to small-scale turbulence thus call for further investigations.

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