

Dear Editor of Biogeosciences,

We would like to thank the two reviewers for their reviews of our revised manuscript "Turbulence measurements suggest high rates of new production over the shelf edge in the north-eastern North Sea during summer". We have addressed all the minor issues raised by the reviewers in the revised manuscript.

Reviewer #1 suggested an analysis of the temporal variability of the timeseries data shown in the supplementary material. This has to some extent already been addressed in the supplementary material but we did not describe these results in detail in the main text. Therefore, this may not have been clear for the reviewer. We now include a reference to these results in the main text. In addition, there was a reference to a table in the legend to figure 6 which led to some confusion about where these data were to be found. We have now made a simpler and more straightforward description of this.

Reviewer #1 also commented on the distribution of maximum nitrate fluxes. This information can be obtained from figures 7c and 3 and we have clarified this in the text. Finally, we acknowledge reviewer #1's interesting considerations about the role of meso-scale variability along the shelf-edge indicated by the satellite images and believe this is something that should be studied further.

Reviewer #2 had a general comment on the description of the nitrate fluxes and also that it should be clarified that references to numerical values in previous studies were temporal averages (this point was also mentioned by #1). We agree on this issue, and we have clarified this when we compare our results with earlier work. Reviewer #2 also asked for examples of the incubation results and we have added an extra figure in the supplementary material showing the results from the first three stations on the cruise where we made these incubations. We also include the results from these incubations shown in the figure legend to figure S2. We have made minor improvements of figure 1 (color scale) and figure 5 (adding small arrows above 5b) and clarified the text according to the suggestions by the reviewers.

We believe the manuscript has been significantly improved by the careful reviews and constructive comments from the two anonymous reviewers and we acknowledge this in the manuscript.

Our detailed response (in normal font) to the reviewer's comments (shown in italics) is enclosed below and a version of the manuscript with "track changes" is also enclosed for your reference.

I am looking forward to hearing from you.

Kind regards,  
Jørgen Bendtsen

## **Reviewer #1**

*Suggestions for revision or reasons for rejection (will be published if the paper is accepted for final publication)*

*Thank you to the authors for a well-structured response to the earlier review.*

*Most of the queries I had have been answered/clarified. I have just a few final points:*

*1. I still do not fully understand how the individual, single-cast turbulence measurements (or averages based on a handful of closely-spaced single profiles) compare to the tidal variability seen at the time series station. Tides are clearly important in determining the variability in mixing, but this has not been fully explained. In Fig. S1 there appears to be sufficient data to calculate an average turbulence profile with a measure of variability (e.g. 95% confidence intervals using a bootstrap technique on the profiles). Then comparing average profiles and confidence intervals based on a handful of closely-spaced stations elsewhere in the survey would be useful in indicating if there were significant contrasts in mixing outside of the tidal variability. This is different to the analysis done on the paired shear probes (which is a nice, robust QC of the data, but doesn't tell us about tidal variability).*

Response:

We include an analysis of the temporal variability observed at time series station T1 described in the supplementary material. The variability of the time series is analysed in vertical bins of 5 m intervals in the first part of the time series, i.e. the first 11 casts over 30 minutes, to provide information about the temporal variability between subsequent casts. It is found that the variability (ranging between 1.4 - 2.1  $10^{-9}$  W kg<sup>-1</sup>) is well below the range observed in the data set. This result supports our argument that the individual casts along the transects are representative for the conditions when considered over a similar time period. From the current data set, we cannot analyse the general influence of tides along the transects and we do not make any conclusions about the influence from tidal currents, although we discuss their likely influence on mixing in the area (for example in relation to Figure 8). The suggestion by the reviewer is partly covered by the calculation in the supplementary material and we have added a more specific reference to this in the parenthesis in the following sentence (p4, l27): "Short term variation at T1 was also found to be relatively small and temporal changes between subsequent casts were considered to have a little influence on the calculated  $\epsilon$ -values (time series analysis in Supplementary material)". However, we cannot address the influence from tidal currents on the spatial distribution of nitrate fluxes from the present data set. We show that tidal currents likely play an important role for the temporal variability at time series station 2 (Fig. 8) but we also discuss that other sources, e.g. meso-scale variability, may be important for mixing along the shelf edge. Considering the transient nature of mixing processes, we find it quite interesting that increased nitrate fluxes are consistently located along the shelf edge. This is not a proof that the shelf edge is the only source of new production in the area but, considering the length of the cruise and number of stations, we find that this pattern is a strong indication that the area plays a very important role for biological cycling in the area.

*In the revised manuscript (section 3.7, page 13) it is stated that turbulence measurements were not made at night. Fig. S1 suggests they were made at night – assuming the DoY 202.0 is midnight. In Fig. 8 it looks like data were indeed not collected for a short time at night.*

Response:

We have added "... no turbulence measurements were made at night at this station ...", to specify and clarify that there were no measurements during night "at this station" (p13, l25). The first timeseries station, analyzed in the Supplementary material, included measurements during the night.

*On page 14, line 10 – I do not understand why the observation that turbulent dissipation was similar to tidal energy dissipation (1st sentence) then suggests that there must be another source of turbulence (2nd sentence). To me the 2nd sentence simply does not follow on from the claim in the 1st sentence.*

Response:

We have clarified the logic in this sentence. We have removed "This suggests that ..." in the following sentence that now reads: "Additional energy for turbulence may also be provided from non-tidal currents along the shelf edge ...".

*Looking at Fig. 5 it does look like additional turbulence in the bottom boundary layer over the shelf edge. Is the claim that this turbulence is not tidal? If not, are there any published reports of slope currents or eddies that could be cited as suggestive of the source of the mixing?*

Response:

We cannot (and do not) claim that the source is not tidal currents. From the data set, we cannot say what the source of energy is for the mixing in the boundary layer. However, we suggest likely energy sources could be tides or currents along the shelf edge. In addition, we describe previous studies in the area in the Introduction where increased meso-scale variability was identified in the region (e.g. the reference to Røed and Fossum, 2004). We are not aware of published reports of slope currents besides the more general descriptions of the circulation pattern in the area obtained from model studies (e.g. described in the references to the four model studies in the Introduction).

*In the supplementary material the vertical turbulence profiles are described as being "3 minutes" apart. But this is not the temporal resolution of the profiles. What is the typical time interval between the start of each profile (i.e. the period of the turbulence profiler yo-yos)?*

Response:

At this time series station, the interval was in fact about 3 minutes. The profiler was lowered to about 50 m and the following cast was repeated when the profiler was brought to the surface again. This operation took about 3 minutes and, in total, 107 casts at the station were made (three persons were continuously in action during this operation).

*2. On page 17 it is now more clearly articulated than the relatively strong turbulent flux of nitrate is a consequence of (1) deeper nutricline and (2) "elevated" mixing. But it is not clear that the increased nutrient flux is at the shelf edge. It might be shown in Fig. 6, but I cannot work out where the profiles in Fig. 6 came from. The caption refers to "summarised in the tables (e-h)". I assume e-h refers to the profiles in Fig. 6, but which "tables"? Neither of the tables in the manuscript have location information. The nitrate flux has a clear peak in profile g, associated with a peak in turbulent dissipation, but it is not clear where on a transect this was. Can the positions of the profiles be marked on one of the earlier sections? Alternatively does this "elevated" shelf edge mixing rest on the evidence of the sections in Fig. 5 (though the relationship to the nutricline is not obvious)?*

Response:

This has been clarified. The "tables" referred to are written as inlets in the figures e-h. Along with profiles from each station, the lower figure also contains information about latitude (to locate the station on the map), nutricline depth and maximum nitrate fluxes. We have replaced the reference to "summarized in the tables (e-h)" with "shown in the figures (e-h)" in the figure legend. This hopefully, clarifies this issue. In addition, we now show the locations of the four stations by arrows

in fig. 5b. The latitudes of the stations shown in the figures can also be related to the maps (figs. 1, 7). The figure legends for figs. 5 and 6 have been modified accordingly.

*In general avoid the word “elevated”. It is ambiguous – do you mean “increased” or “raised upward in the water column”? I’m assuming “increased”....better to make this clearer throughout.*

Response:

We have clarified this and modified the text accordingly.

*3. Line 15, page 17. The largest nitrate fluxes of 1 – 1.5 mmol m<sup>-2</sup> day<sup>-1</sup> are stated (with reference to Fig. 7), but I cannot see the parameters behind these in any of the data presented. Table 2 shows mean fluxes (it does not clearly say where from in the caption), which are very low, and the maximum value I can see in Fig. 6 (g) is about 0.3 mmol m<sup>-2</sup> day<sup>-1</sup>. There only are a handful of points in Fig 7 with these high values of nitrate flux, so without any other information (e.g. profiles of nitrate and turbulence) there is nothing to support the underlying reasons for these fluxes - they could easily be interpreted as outliers. In other words, what is the link between these high flux points, the patterns of turbulence in Fig. 5 and the flux profiles in Fig. 6? Are you attributing these high fluxes to the increased boundary mixing and deeper nutricline idea (see also point 5 below....)?*

Response:

We have modified the reference to the values above the shelf-edge so the reference to figure 7 now reads (p13, 111): "However, the largest nutrient fluxes were seen in the shelf edge zone and near the Norwegian coast. This resulted in f-ratios above 0.10 in these regions compared to < 0.02 for the remainder of the study area (Fig. 7, S2)." We have also clarified that the values in Table 2 are based on the whole data set by adding "...of all data ..." in the caption. The information about the fluxes can be found in figure 7c where the spatial distribution of the maximum flux into the euphotic zone is shown. The vertical distribution of the maximum fluxes along all transects can be seen in figure 3 (orange squares) and the vertical distribution of vertical mixing rates is presented in figure 5 along transect 2 and 4. Finally, the nutrient distribution is shown along transect 4 in figure 2. So, all the pieces of information necessary for understanding the spatial distribution of the nitrate flux are contained in these figures. Figure 6 shows an example of four stations measured within a few hours of each other where all the components in the calculations are shown. We do not consider the measurements along the shelf-edge as outliers and We would also like to emphasise that we do not consider the specific values as being the most aspect of our results. We believe the general pattern where increased nitrate fluxes are located along the shelf-edge indicates that this area has a special significance for NP. Therefore, we have modified the references to specific numerical values of the nitrate flux. We have added more information to the paragraph describing Fig. 7c to relate the results to the other figures and table 2 (Section 3.5, p12, 112): " The vertical distribution of the maximum nitrate flux was, in general, characterized by being located below the SCM (cf. Fig. 3, Table 2). However, the horizontal distribution showed a characteristic pattern where increased fluxes and f-ratios were found along the shelf-edge on Tr2-Tr5" .

*The cited values of nitrate fluxes to the SCM from other shelf studies are all daily-means, so make it clear in the text if you are comparing maximum values with daily means, or daily means with daily means.*

Response:

We have modified the text and specify that the cited values from the two studies are daily averaged values.

4. On page 18 it is stated that the maximum nitrate flux was on average found below the nutricline depth (by 6.4 m). Given the vertical resolution of the nitrate samples, this is not significant. Also, the maximum flux is stated as being below the SCM – but if the SCM depth is defined as the maximum chl concentration, this is not surprising. The peak of typical shelf sea SCM is often coincident with the point where nitrate hits zero (within the constraints of the resolution in this study, that looks like a reasonable claim here as well), so the relevant region over which to look at the nitrate flux is generally in the low part of the SCM rather than at the peak. Nitrate reaching zero at the SCM peak then lends support to the statement that recycling must be important further up in the SCM (or, indeed, motility given the very low turbulence in the SCM).

Response:

We describe the calculation of the nutricline depth in the first paragraph in section 2.5: "To minimise the uncertainty of the nutricline depth estimate associated with the linear interpolation between two neighbouring water samples, the nutricline depth was found by linear interpolation between the corresponding potential density anomalies ( $\sigma_\theta$ ) of the sample depths, and the nutricline depth was then identified from the corresponding  $\sigma_\theta$  in the CTD-profile. This approach is based on the assumption that the nitrate concentrations between two water samples are more closely related to water mass characteristics than linearly to depth changes, i.e. a sharp pycnocline, not resolved by the water samples, is taken into account when the nutricline depth is estimated by this method." Thus, the nutricline depth is calculated at the same resolution as the CTD-profile (the CTD sampled at 24 Hz and was bin-averaged every 0.5 m) and, therefore, the result that the nutricline depth is located, on average, 6.4 m below the SCM is significant. This is actually a quite interesting result as it implies a transport between the SCM and the maximum N-flux. We agree in the reviewer's considerations related to this about regenerated production in the lower part of the euphotic zone and the possible influence from motility.

5. The addition of the satellite imagery is really interesting. It looks to me (comparing Figs 1 and 7) that the high values of nitrate flux are coincident with fronts in SST associated with what might be an outflow from the Baltic. I have no idea if this is coincidence or causal, but could this be tentative evidence of another source of flow and shear in the system? In relation to my point 3 above, could the mechanism underpinning these highest fluxes that you see be different from the boundary-driven turbulence plus deeper nutricline idea? The more I look at the data, the more I think there may be two mechanisms behind the pattern of nitrate fluxes: (1) shelf edge boundary mixing combined with deeper nutricline for the "typical" fluxes of 0.1- 0.3 mmol m<sup>-2</sup> day<sup>-1</sup>, and frontal or mesoscale shear associated with the warm surface water from the Baltic driving the larger fluxes (which are patchy in the survey data, but could be quite significant given the scale of the SST signal). So the highest f-ratios might be frontal signatures. Obviously (!) don't try to open up a new area of analysis – but there may be published work on Baltic outflows to the N Sea that might help justifying this as a reasonable hypothesis in the discussion.

Response:

This is a very interesting comment and we agree in that meso-scale variability associated with outflowing water from Skagerrak may contribute with frontal mixing in addition to mixing associated with dynamics at the shelf-edge. We have not considered this further in this study but the role of various mixing processes on the production and ecosystem structure in the area is the subject of on-going studies. Regarding previous studies, we are not aware of studies focusing on this issue in detail. There are several model studies describing the general circulation in the area (cf. our response to comment no. 1 above and the cited references) but they do not describe the outflow dynamics and mesoscale variability in detail.

## Reviewer #2

*Suggestions for revision or reasons for rejection (will be published if the paper is accepted for final publication)*

*The authors correctly addressed my main concerns and the revised manuscript was significantly improved. The revised manuscript includes, among others, a more thorough evaluation of the uncertainties associated with the TKE dissipation and nitrate fluxes (extended Figure 6) calculations; new panels in Figures 2 and 7 displaying the distribution of nitrate in transect Tr4, and the distribution of nitrate fluxes across the shelf edge; microstructure and CTD data from a 36-hour time-series, and a Table presenting the median of relevant parameters for the different regions. Those modifications strengthen the communication of the manuscript's main conclusions. I have only a set of relatively minor points that I would like the authors to address before the manuscript is published.*

### *GENERAL COMMENTS:*

*I contend that some weaknesses remain in the communication of the main conclusions. See for example the following sentences:*

*“Estimated nitrate fluxes due to turbulent vertical mixing into the euphotic zone were up to 0.5 - 1 mmol N m<sup>-2</sup> d<sup>-1</sup> over the shelf-edge (f-ratios > 0.1) while values of < 0.1 mmol N m<sup>-2</sup> d<sup>-1</sup> were found in the deeper open area north of the shelf-edge.” (Abstract, P.1 L. 13-14)*

Response:

We have specified that the results show that large values were found above the shelf edge and modified the sentence accordingly to the following: "

Relatively large (up to >0.5 mmol N m<sup>-2</sup> d<sup>-1</sup>) nitrate fluxes due to turbulent vertical mixing into the euphotic zone were found at some stations over the shelf-edge, while low values (< 0.1 mmol N m<sup>-2</sup> d<sup>-1</sup>) were found in the deeper open area north of the shelf-edge. "

*“Nitrate fluxes were generally very low (< 0.1 mmol N m<sup>-2</sup> d<sup>-1</sup>) in the deeper area north of the shelf edge due to low vertical mixing in the upper 50 m. However, elevated nutrient fluxes of ~1 mmol N m<sup>-2</sup> d<sup>-1</sup> were seen in the shelf edge zone and near the Norwegian coast. This resulted in f-ratios above 0.10 in these regions compared to < 0.02 for the remainder of the study area (Fig. 7, S28d, e).” (P. 14, L. 10-14)*

Response:

We have reformulated the sentence without specifying the numerical value of 1 mmol N m<sup>-2</sup> d<sup>-1</sup>. The sentence has been changed to: ..." However, the largest nutrient fluxes were seen in the shelf edge zone and near the Norwegian coast. ...."

*“Significant NP was found above the shelf-edge where vertical nitrate fluxes of 0.5 - 1.5 mmol N m<sup>-2</sup> d<sup>-1</sup> implied f-ratios above 0.10, whereas very low nutrient fluxes characterised the open area above the Norwegian Trench (f-ratios < 0.02).” (Conclusions, P. 21, L. 15-17)*

Response:

We have reformulated the sentence accordingly to the following: "Significant NP was found above the shelf-edge where, at some stations, relatively large nitrate fluxes, i.e. > 0.5 mmol N m<sup>-2</sup> d<sup>-1</sup> implied f-ratios above 0.10. "

*Although the nitrate diffusive flux was as high as ~1 mmol m<sup>-2</sup> d<sup>-1</sup> and f>0.10 in some stations*

*over the shelf edge area, those values seem not to be representative of the “mean state”, according to the median values presented in Table 2. The median flux in the shelf edge area and the corresponding f-ratio (0.11 mmol m<sup>-2</sup> d<sup>-1</sup>, f-ratio = 0.021) are well below the values reported in these sentences. I would suggest to rephrase the sentences to acknowledge that, although values of the f-ratio/nitrate fluxes at individual stations could be as high as 0.1 and 1 mmol m<sup>-2</sup> d<sup>-1</sup>, those values do not correspond to the regional means.*

Response:

We have reformulated the sentences above to reflect that the distributions are characterised by the large values along the shelf edge.

**SPECIFIC COMMENTS:**

*- This sentence “Every cast provided two shear-measurements and, in general, there was relatively small deviation between the two shear probes. Therefore, all measurements were included in the analyses and values from the two shear-probes were averaged.” (P.4, L 20) seems contradictory with the following paragraph (“This led only to the removal of a few pairs of epsilon from the dataset”, P.4, Line 32)*

Response:

This has been corrected and clarified. The sentence is a reminiscence from the first version of the manuscript and was, unfortunately, not deleted. The new quality check applied in the revised version is described in detail in the paragraph below.

*- Although I think that I understand what the authors meant with these two sentences: “ Thus, PBmax was significantly lower at the SCM, in general accordance with previous studies (see review in Richardson et al., 2016) whereas  $\alpha_B$  showed a weak decrease with depth (with overlapping uncertainty intervals between the two depth levels). In general,  $\alpha_B$  has been found to increase with depth (resulting in a more efficient photosynthetic response at low light levels) and inspection of the vertical distribution showed a tendency to higher values between 15 -25 m depth (i.e. 2 - 3 e-folding depth of PAR) and lower values below 30 m resulting in a lower median value from SCM level.” (P. 12, L. 15-19); they might also sound a bit contradictory and probably need some clarification.*

Response:

We have clarified this issue further by adding "significantly" to the sentence: "In general,  $\alpha_B$  has been found to increase significantly with depth ....". The sentence is a general consideration about the distribution of  $\alpha_B$  in relation to global measurements from various areas. An interesting aspect, however, is that a similar vertical distribution was reported in the cited study of Hickman et al. in the Celtic Sea.

*- In P 14, Line 5: “cf. Fig. 2c,d” I think the authors wanted to refer to Supplementary Figure 2 here. Also, the description of the figure remains extensive in the text. Although it contains some repeated information, I would also agree if the authors decided to keep this figure (or a reduced version of it) in the main manuscript file. My main concern with this figure was that the cross-shelf variability of the nitrate fluxes was nuanced here, but this is now clearly illustrated in Figure 7c.*

Response:

We prefer to keep the figure in the supplementary material because the distributions are now shown in the panels in figure 7 and figure 3 (nutricline depth). However, the figure also shows the temporal variability and, although this is not a main finding in relation to this analysis, it is a relevant piece of information.

*- I appreciate that the authors extended the discussion about the calculation of photosynthetic parameters and its uncertainties. However, I still would like to see how the fitted curves and the data actually look like, as they are a central point of the manuscript. Could you show some figure as example to me and, maybe, include them in the manuscript or as supplementary information?*

Response:

We have included examples from the first three stations in supplementary figure S2. The figure shows incubations from the surface sample (5 m) and the SCM at the three stations. The non-linear fits are shown (lines) and the associated values of the photosynthetic parameters are listed in the figure legend. Similarly good fits were obtained from the other incubation stations. We have added a reference to the figure in the Methods section and in the first paragraph in section 4.2.

*-Figure 7 (caption): Could you add the integration depth in the Figure caption as well?*

Response

This has been added.

*- Table 2 (caption). "...depth intervals of depth," , please remove one "depth"*

Response:

This has been corrected.

# Turbulence measurements suggest high rates of new production over the shelf edge in the northeastern North Sea during summer

Jørgen Bendtsen<sup>1</sup>, Katherine Richardson<sup>2</sup>

5 <sup>1</sup>ClimateLab, Symbion Science Park, Copenhagen, 2100 O, Denmark

<sup>2</sup>Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, 2100 O, Denmark

*Correspondence to:* Jørgen Bendtsen (jb@climatelab.dk)

**Abstract.** New production, i.e., that driven by allochthonous nutrient inputs, is the only form of primary production that can lead to net increases in organic material and is, therefore, important for understanding energy flow in marine ecosystems. The spatial distribution of new production is generally, however, not well known. Using data collected in July, 2016, we analyse the potential for vertical mixing to support new production in the upper layers of the northeastern portion of the North Sea. Relatively large (up to  $>0.5 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) ~~Estimated~~ nitrate fluxes due to turbulent vertical mixing into the euphotic zone were found at some stations over the shelf-edge, up to  $0.5 - 1 \text{ mmol N m}^{-2} \text{ d}^{-1}$  over the shelf edge (f-ratios  $> 0.1$ ) while low values ~~of~~ ( $< 0.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) were found in the deeper open area north of the shelf-edge. The low vertical mixing rates (dissipation rates of turbulent kinetic energy below  $10^{-8} \text{ W kg}^{-1}$ , corresponding to vertical turbulent diffusion coefficients of  $10^{-6} - 10^{-5} \text{ m}^2 \text{ s}^{-1}$ ) implied f-ratios of  $< 0.02$  in the open waters north of the shelf-edge. In the shallow ( $< 50 \text{ m}$ ) southern and central part of the study area, inorganic nutrients were low and nitrate undetectable suggesting negligible new production here, despite relatively high concentrations of chlorophyll a being found in the bottom layer. Thus, high rates of new production seem to be concentrated around the shelf-edge zone and in association with localised features exhibiting enhanced vertical mixing. We find that the nutricline depth is significantly deeper at the shelf edge and interference with increased mixing in this deeper depth range can explain the increased diapycnal nitrate fluxes. Overall, this suggests that the shelf-edge zone may be the major nutrient supplier to the euphotic zone in this area during the period of summer stratification.

## 1 Introduction

25 New Production (NP), i.e. primary production (PP) based on inorganic nutrients recently introduced to a system, balances net losses of organic material in the euphotic layer when considered over longer periods (Dugdale and Goering, 1967). Net loss of biomass from the surface layer may be due to sinking phytoplankton or transfer to, and subsequent losses from, higher trophic levels such that this cycle between nutrient input, PP and remineralisation of organic matter constitutes an organic biological pump in the upper ocean (Volk and Hoffert, 1987). In addition to NP, total PP is comprised of photosynthesis driven

by nutrients recycled within the system, itself. The ratio of NP to total PP is referred to as the f-ratio (Eppley and Peterson, 1979). This ratio is known to vary both seasonally and spatially.

5 Given that NP can lead to a net increase of organic material, its occurrence can be expected to have important consequences for food webs and the distribution of marine organisms. Scott et al. (2010) analysed the distribution of marine mammals and seabirds in the northwestern North Sea and they found the distribution of these organisms to be best explained by the presence of a sub-surface chlorophyll maximum (SCM). They furthermore speculated that bathymetric features induced vertical mixing that could bring nutrients to depths containing the chlorophyll peak, which then could lead to localised NP. This potential link between localised increased NP in sub-surface layers and the highest trophic levels may, therefore, be an important feature in ecosystem functioning. The distribution of NP, especially over small spatial scales, is however not well understood. The purpose of this study, therefore, was to describe the potential for NP based on the vertical mixing of nutrients into the euphotic zone to occur in the northeastern North Sea, a highly productive temperate ocean region. The summer season was chosen for the study as this region is thermally stratified at this time and surface waters characterised by low or undetectable concentrations of inorganic nutrients and low phytoplankton biomass. Thus, it is generally assumed that little NP is occurring in these waters at this time.

The northeastern North Sea is characterised by the transition from a relatively shallow southern region (depth ~ 40 m) across a shelf-edge (depth ~80 - 130 m) towards the deep (> 400 m) Norwegian Trench leading into Skagerrak (Fig. 1). The general cyclonic circulation is characterised by inflow from the Atlantic along the shelf-edge, either from mainly wind-driven inflow between the Shetland and Orkney Islands or from transports along the Norwegian Trench (Winther and Johannessen, 2006). Outflow takes place along the Norwegian coast, partly as less saline water masses in the Norwegian Coastal Current, and with an estimated net transport of about 1 Sv in either direction (Danielssen et al., 1990). The relatively large cyclonic flow has also been found in model studies (Winther and Johannessen, 2006; Pätzsch et al., 2017) where current speeds along the northeastern shelf-edge towards the Skagerrak intensify (Holt and Proctor, 2008) and are found to be associated with a large eddy-activity (Røed and Fossum, 2004). This dynamic area was chosen as the study area as it is a potential location for increased vertical mixing and nutrient transports due to, for example, eddy-activity, breaking internal waves, and upwelling at the shelf-edge.

A large part of the central and northern North Sea becomes stratified during the summer season with an SCM between ~20-40 m depth. Richardson et al. (2000) found that a significant amount of PP occurs at the SCM and argued that much of this could be NP supported by fortnightly tidally driven input of nutrient rich deep water to the SCM. Fernand et al. (2013) found that up to 60% of PP took place in the SCM in the central and northern North Sea during the summer. Those workers also reported a distinct SCM in the northern North Sea where the depth was larger than ~40 m, i.e. areas where tidally induced mixing cannot break the stratified water column. The northern North Sea is relatively productive during the summer season with PP levels of

~0.5 - 0.9 g C m<sup>-2</sup> d<sup>-1</sup> (Weston et al, 2005; Fernand et al., 2013). However, few studies have been made of PP at the northern shelf-edge and the distribution of NP is unknown.

Shelf areas, in general, constitute an important link between the large reservoirs of dissolved substances in the open ocean and coastal water masses and shelf processes play an important role in global cycles of nutrients, oxygen and carbon (Gattuso et al., 1998). Transports across the shelf edge bring nutrient-rich deep-water masses into more shallow and well-mixed areas and stimulate production above the shelf. Various cross-shelf transport processes can facilitate this exchange (Brink, 2012), thus different exchange processes may dominate in different shelf-edge regions. However, shelf-edge areas share common dynamical features due to their relatively steep bathymetric slopes and the separation between coastal and open ocean water masses. Therefore, the conditions in the north eastern North Sea may be representative for similar shelf-edge regions not directly exposed to the open ocean basins.

Here, we analyse the physical and biological processes affecting PP and NP during the stratified summer period across the shelf-edge in the northeastern North Sea based on data collected during the VERMIX cruise in July 2016. First, we describe the distribution of water masses, nutrients and vertical mixing in the area. Then, we present results from PP-incubations and, based on averaged representative photosynthetic parameters, calculate PP for the whole study area. Nitrate fluxes and NP are calculated and compared with PP to derive f-ratios. Finally, the implications for NP in the North Sea are discussed.

## 2 Methods

### 2.1 Study area and hydrographic measurements

The VERMIX study covered an area around the shelf-edge in the north eastern North Sea from the shallow shelf area (depth <50 m) across the western part of the Norwegian trench (~500 m) towards the coast of Norway (Fig. 1 a). In this study, we define the shelf-edge zone as being where depths are between 80 m and 130 m and refer to areas south and north of this zone as the shallow shelf area (<80 m) and the area off the shelf edge zone (>130m), towards Norway, respectively.

The cruise was carried out on board R/V Dana (Technical University of Denmark) during the period 12 - 31 July 2016. Stations were placed along five transects between 56.2 - 57.8° N and along 8.25° E (Tr1), 7.75° E (Tr2), 7.25° E (Tr3), 6.75° E (Tr4) and 6.25° E (Tr5), respectively (i.e. ~25 km between transects). Wind and light conditions were typical for the period with windy conditions during the first week (along Tr1 and Tr2 with wind speeds up to 20 m s<sup>-1</sup>) and relatively calm conditions during the rest of the cruise (Tr2-5). In total, 132 stations were sampled along the transects with a general distance between stations of 10 km and at sections along Tr2 and Tr4 this distance was decreased down to ~1 km. Measurements along these two transects were made several times during the cruise to examine temporal variability. Measurements over 22 - 36 hours

were made at two time series stations (T1, T2) located at Tr2 and Tr4, respectively. Hydrographic measurements of conductivity, temperature and depth (CTD) were made with a Seabird SBE911 plus system, including two sets of temperature, conductivity and oxygen sensors (SBE43) and equipped with a SCUFA fluorometer, a PAR-sensor (Licor) and 12 Niskin bottles (30 l) for water sampling. All salinity values are reported as practical salinity ( $S_p$ ) and referred to as salinity (S) and TEOS10 (IOC et al., 2010) was applied for calculating properties of seawater.

## 2.2 Measurements of turbulence and micro-structure

Micro-scale turbulence was measured with a loose-tethered free-fall Rockland Scientific International (RSI) VMP-250 microstructure vertical profiler equipped with two shear probes, a FP07 thermistor and a micro-conductivity sensor. Microstructure of temperature and salinity only supported the analysis of shear-induced turbulence and are not discussed further here. The profiler was also equipped with a CT- and pressure-sensor (JFE Advantech). The JFE-CTD data were binned in 0.1 dbar and the conductivity sensor was aligned with temperature by a delay of 0.14 s. Microstructure measurements were made at 512 Hz and stored at 64 Hz and the CT-sensor operated at 16 Hz. Turbulence profiles were obtained while the ship was freely drifting. In total, 253 casts down to about 5 m from the bottom, or to a maximum depth of 200 m above deeper areas, were made during the cruise. Every cast provided two shear-measurements ~~and, in general, there was relatively small deviation between the two shear probes. Therefore, all measurements were included in the analyses and values from the two shear probes were averaged.~~ T and the dissipation rate ( $\epsilon$ ) of turbulent kinetic energy (TKE) was calculated with software provided by Rockland Scientific. Dissipation of TKE was estimated from below 10 m depth in order to exclude possible disturbances from the ship (depth of ship was 5.7 m) and analysed in bins of 8 seconds with 50% overlap, corresponding to a resolution of  $\sim 3$  m, following the method described by Wolk et al. (2002) and revised by Lueck (2016).

20

The uncertainty and short-term temporal variability of the calculated  $\epsilon$ -values were assessed from a time series station (T1) at Tr2 where  $\epsilon$ -values were calculated from 107 casts carried out in three sequences over a 22 hours period (Supplementary material). In general, there was good accordance between estimates of  $\epsilon$  obtained from the two sensors and the error-distribution, defined from the difference of the logarithm (to the base 10 and in units of  $W\ kg^{-1}$ ) between the two estimates, had an absolute standard deviation of 0.14 (Fig. S1). In order for measurements to be included in the analysis, we applied the criterion that the difference between the measurements made by the two sensors on a single profile should be less than three times the absolute deviation. This led only to the removal of a few pairs of  $\epsilon$  from the data set. Short term variation at T1 was also found to be relatively small and temporal changes between subsequent casts were considered to have a little influence on the calculated  $\epsilon$ -values (time series analysis in Supplementary material). Therefore,  $\epsilon$ -values were, in general, derived from a single cast between the relatively closely spaced stations, and the  $\epsilon$ -value obtained by averaging the calculated value from the two shear-probes was reported.

30

The vertical turbulent diffusion coefficient ( $k_v$ ) was estimated from the dissipation rate of TKE (Osborn, 1980):

$$k_v = \Gamma \frac{\varepsilon}{N^2} \quad (1)$$

with a mixing efficiency ( $\Gamma$ ) and the Brunt-Väisälä frequency ( $N^2$ ) determined by linear regression of density ( $\rho$ ) with depth in 10 m intervals:

$$N^2 = -\frac{g}{\rho_0} \frac{\partial \rho}{\partial z} \quad (2)$$

where  $\rho_0$  is a reference density ( $1027 \text{ kg m}^{-3}$ ) and  $g$  is the gravitational acceleration.

The mixing efficiency,  $\Gamma$ , is here assumed constant and equal to 0.2 and this is within the range  $\Gamma \leq 0.20$  suggested by Osborn (1980). The value of 0.2 is supported by numerical studies when the turbulent intensity, defined by  $Re_b = \varepsilon / (\nu N^2)$  where  $\nu$  is the molecular viscosity, is within the range 7-100 (Shih et al., 2005), and the model by Bouffard et al. (2013), also validated against field data, finds the valid range to be between 20 and 400. Outside this mixing regime, the mixing efficiency is less than 0.2. We apply the range of Bouffard et al. (2013) and this implies that our calculated diffusion coefficients with a constant mixing efficiency of 0.2 are valid in the range between  $0.5 \cdot 10^{-7} - 1.0 \cdot 10^{-4} \text{ m}^2 \text{ s}^{-1}$  (we use  $\nu = 1.2 \cdot 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ). This range encompasses the data used for calculating vertical nitrate fluxes in the euphotic zone in our study.

### 2.3 Measurements of nutrients and chlorophyll a

Water samples were taken at CTD stations from standard depths (5, 10, 30, 40, 60, 100, 200 m and close to the bottom). In addition, a sample from the depth (i.e. peak) of the subsurface chlorophyll a maximum (SCM) was sampled. At some stations, a distinct second chlorophyll peak or “extreme” (i.e. a subsurface chlorophyll a extremum, SCE) was observed above the SCM. In some cases, water for photosynthesis incubations and inorganic nutrient (nitrate, nitrite, ammonia, phosphorous and silicate) determination was taken from these SCEs. However, in this study we refer only to subsurface samples from the SCM. Water samples for nutrient determination were tapped from the Niskin bottles and immediately frozen. The sample was subsequently thawed, filtered (Milipore Millex-GP Hydrophylic PES  $0.22 \mu\text{m}$ ), and analysed for nitrite, nitrate, ammonia, phosphorous and silica by wet-chemistry methods according to Grasshoff (Ed.) et al. (1983) (detection limits were 0.04, 0.1, 0.3, 0.06 and  $0.2 \mu\text{M}$ , respectively) at Aarhus University, Department of Bioscience. In total 649 water samples were analysed for nutrients.

Chlorophyll a (GF/F filtered and extracted in 90% ethanol) was determined fluorometrically (Trilogy, Turner Designs) and used to calibrate the rosette mounted fluorometer (chlorophyll a is simply referred to as chlorophyll below). A relatively constant background fluorescence was measured in the deep profiles ( $>200 \text{ m}$ ). As we see no reason for a constant distribution of chlorophyll in waters down to depths of  $\sim 500 \text{ m}$ , we considered this fluorescence to be generated by material other than chlorophyll. Therefore, the fluorescence was averaged between 100-500 m at a deep station on Tr1 ( $57.83^\circ \text{N}$ , average value of  $0.023 \text{ volt}$ ). This relatively small value was treated as an unknown background and subtracted from the fluorescence signal

(F). The chlorophyll concentration (chl, mg chl m<sup>-3</sup>) was then determined from a linear regression between fluorescence (F) and filtered chlorophyll samples as  $chl = 3.23 F - 0.08$  ( $R^2 = 0.71$ ,  $n = 205$ ).

## 2.4 Calculation of photosynthetic parameters and PP

Primary production (PP) was determined from incubations made with Photosynthetic Available Radiation (PAR) at 12 different light intensities from 0 - ~800  $\mu\text{E m}^{-2} \text{s}^{-1}$ . In total, 64 incubations were made with water sampled from the surface and/or SCM at 41 stations and 23 and 25 incubations were selected to represent the conditions at the surface (5 m) and SCE, respectively (Table 1). Total PP was then calculated according to Platt et al. (1980):

$$PP(chl(z), PAR(t, z)) = \int_{24h} \int_{-Deu} P_{max}^B(z) chl(z) \left( 1 - \exp\left(-PAR(t, z) \frac{\alpha^B(z)}{P_{max}^B(z)}\right) \right) \exp\left(-PAR(t, z) \frac{\beta^B(z)}{P_{max}^B(z)}\right) dz dt \quad (3)$$

where the integral is carried out in the vertical ( $z$ ) from the euphotic depth,  $Deu$ , (assumed to be 0.1 % PAR, see below) to the surface and during a 24-hour period ( $t$ ). The photosynthetic parameters ( $P_{max}^B$ ,  $\alpha^B$  and  $\beta^B$ ) were determined by fitting the photosynthesis (P) vs. E curves generated from the incubations to the PP expression, i.e. the terms in the integral in Eq. (3), by a non-linear Levenberg-Marquardt least-squares routine (Press et al., 1992) and normalised with *in situ* chlorophyll concentration obtained from the calibrated CTD-fluorescence measurement. The case without photo-inhibition, i.e.  $\beta = 0$  (Webb et al., 1974), in general, resulted in a poorer representation of the data (except for six incubations where the photo-inhibition term was set to zero) and the incubation experiments were, therefore, analysed with the photo-inhibition term included in Eq. (3). These model fits were found to be in very good accordance with the incubation data (Fig. S2). The maximum rate of photosynthesis, defined as  $P_{max}^{B*}$ , was calculated for each P vs. E curve (note that  $P_{max}^B$  only describes the maximum PP in the case without photo-inhibition).

20

Irradiation was measured continuously during the cruise and the hourly averaged insolation curve during the day was scaled to equal the daily averaged photosynthetically available radiation (PAR) measured from the MODIS-Aqua satellite measurements (Frouin et al., 2012) where the daily averaged PAR for July 2016 in the study area (13-28 July, 6.2° - 8.3° E, 56.2° - 58° N) was 506  $\mu\text{E m}^{-2} \text{s}^{-1}$ . The vertical light extinction coefficient ( $k_d$ ) was determined by linear regression of the log-transformed PAR-measurements from each CTD-cast. The average value from all the CTD-casts was found to be  $k_d = 0.1439 \pm 0.034 \text{ m}^{-1}$  (std.dev,  $n=177$ ), corresponding to a 0.1 % PAR depth level of 50 m. The 0.1 % PAR depth level was in this study assumed to represent the bottom of the euphotic zone.

25

Primary production estimates at individual sites are dependent upon the value for maximum rate of photosynthesis ( $P_{max}^B$ ). However,  $P_{max}^B$  (and all other measured photosynthetic parameters) represents the physiological condition of the phytoplankton community at the time of sampling. This means that  $P_{max}^B$  may vary as a function of time of sampling

30

(Richardson et al., 2017) or during different light conditions (e.g., photo-inhibition). Normalisation of the photosynthetic parameters with chlorophyll also represents an uncertainty in the PP estimates at individual stations as, for example, division with low chlorophyll values (e.g. some surface values were  $\sim 0.1 \text{ mg chl m}^{-3}$ ) may result in large uncertainty of the normalised values due to relatively large absolute errors. This uncertainty error has been shown to potentially have a significant impact on the estimation of photosynthetic parameters (e.g., Kumari, 2005; McKee et al., 2015). Finally, the fact that photosynthetic parameters were determined from incubations carried out on only one water sample from each sampling depth represents a source of uncertainty with respect to the estimates of PP at individual stations. Therefore, in order to compare PP estimates from the stations we sampled, we applied average values (median for all stations) of photosynthetic parameters in the surface layer (5 m) and in the SCM in the calculation of PP. The uncertainties associated with the photosynthetic parameters are further considered in the Discussion. Surface values were assumed to represent the photosynthetic parameters in the upper 10 m and average values from the SCM were assumed to represent the parameters for the water column below 10 m.

## 2.5 Vertical nutrient fluxes and f-ratios

Nitrate was depleted in the surface layer at almost every station and, therefore, assumed to be the limiting nutrient. This assumption was supported by the distribution of other nutrients (shown below). The nutricline was defined as the depth where nitrate equalled  $0.5 \mu\text{mol kg}^{-1}$  (the chosen threshold value had, in general, only a minor influence on the nutricline depth because nutrients were so depleted in the surface layer). In general, water samples were taken close to the nutricline, i.e. within  $\pm 10$  m. However, at 5 stations where the nutricline was not resolved well by the sampling depths, samples from the neighbouring station (i.e. within 5-10 km) were included to increase the resolution. To minimise the uncertainty of the nutricline depth estimate associated with the linear interpolation between two neighbouring water samples, the nutricline depth was found by linear interpolation between the corresponding potential density anomalies ( $\sigma_\theta$ ) of the sample depths, and the nutricline depth was then identified from the corresponding  $\sigma_\theta$  in the CTD-profile. This approach is based on the assumption that the nitrate concentrations between two water samples are more closely related to water mass characteristics than linearly to depth changes, i.e. a sharp pycnocline, not resolved by the water samples, is taken into account when the nutricline depth is estimated by this method. A comparison was made for the whole data set between nutricline depth estimates based on linear interpolation using depth and potential density anomaly levels, respectively. The difference between the two methods averaged  $-1.4 \pm 2.5$  m (std. dev.,  $n=77$ ) and the differences ranged between  $-9.9$  -  $2.4$  m. Thus, in general, the depth level-based method resulted in a deeper nutricline ( $-1.4$  m) than the applied  $\sigma_\theta$ -method.

At all stations where nitrate was present ( $n=73$ ), the nutricline was found to be located above the depth of the 0.1% PAR light level and, therefore, the flux of nitrate ( $F_{\text{NO}_3}$ ) for NP was found by calculating the maximum flux into the euphotic zone (only

transports from vertical turbulent mixing were measured, thus, contributions from vertical advection were not considered).

The vertical nitrate flux ( $F_{NO_3}$ ) due to turbulent mixing is defined as:

$$F_{NO_3} = -k_v \frac{\partial NO_3}{\partial z} = -k_v \frac{\partial NO_3}{\partial \rho} \frac{\partial \rho}{\partial z} \quad (4)$$

where the vertical nitrate gradient is reformulated in terms of density (Sharples et al., 2007). By applying this reformulated  
5 relationship, together with the definition of the vertical turbulent diffusion coefficient in Eq. (1), an expression for the nitrate  
flux in terms of the measured dissipation rate of TKE becomes:

$$F_{NO_3} = \frac{\Gamma \varepsilon \rho_0}{g} \frac{\partial NO_3}{\partial \rho} \quad (5)$$

The advantage of this expression, compared to simply applying  $k_v$  and the vertical nitrate gradient directly, is the dependence  
on the measured dissipation rate, rather than the derived  $k_v$ -value. The latter includes the calculation of the Brunt-Väisälä  
10 frequency, cf. Eq. (2). This term becomes close to zero in very turbulent conditions and, thereby,  $k_v$  becomes sensitive to  
rounding errors and other uncertainties in the measurements. The gradient of nitrate at a given depth was determined linearly  
from the nearest water sample depths.

PP was related to the vertical nitrate flux by estimating the f-ratio, calculated as:  $f = \eta_{N:C} F_{NO_3}/PP$ , where  $\eta_{N:C}$  is the Redfield  
15 ratio between nitrogen and carbon, i.e. 16:106 (Redfield et al., 1963).

### 3 Results

#### 3.1 Water mass distributions

The northern North Sea is a region in which North Atlantic water transported towards the Skagerrak, water masses formed in  
the shallower part of the North Sea and outflowing low-saline water from the Baltic Sea come together. Water masses and the  
20 general circulation in the area have been described by Danielssen et al. (1990), and the general water mass characteristics they  
identified are included in the description below. Their analysis was based on measurements obtained in the Skagerrak and the  
northeastern North Sea in 1990-91.

The inflow of Atlantic water to the northern North Sea, in general, takes place between the Orkneys and Shetland, above the  
25 shelf east of the Shetland and in the deep Norwegian channel and the deep inflow in the Norwegian channel dominates during  
the summer period (Winther and Johannesen, 2006). Atlantic water masses (AW) are characterised by salinities  $> 35$  and can  
be further delineated as upper Atlantic water (AWu,  $S = 35.00 - 35.15$  and  $T = 8 - 10$  °C) and a slightly colder and more saline  
deeper Atlantic water mass (AWd,  $S = 35.15 - 35.32$ ,  $T = \sim 7 - 10$  °C, Fig. 1b). The AWd was observed on the westernmost  
transects (Tr4 and Tr5) between 100 - 300 m along the shelf edge. High saline AWd was also present in the depth range 120 -  
30 200 m on Tr1 (not shown). AWu was observed at the shelf edge at depths below 60 m on Tr2 - 5 whereas it was found at

depths below 80 m on Tr1 (Fig. 2). An upward doming of the AWu was seen to reach to ~ 30 m between the shelf-edge and the Norwegian coast from where isotherms and isohalines tended to deepen towards Norway. Central North Sea water (CNSW,  $S = 34.80 - 35.0$  and  $T = 8 - 10$  °C), a mixture of Atlantic water and Scottish coastal water, was located above AWu and a distinct frontal zone between the two water masses was seen along the shelf-edge where bottom depths ranged between 40 and 5 60 m.

The influence of southern North Sea water (SNSW,  $S = 34.50 - 34.8$ ,  $T = 8 - 12$  °C) (note the larger temperature interval in mid-summer than defined in Danielssen et al. (1990)) and low nitrate concentrations, originating from the English Channel, was seen at the shallower stations ( $< 40$  m) on all transects except Tr1. Warm subsurface water between 20 - 40 m at Tr1 10 indicated an influence from the Jutland coastal water mass (JCW,  $S = 32 - 34$  and  $T = 10 - 15$  °C) on this transect. The surface mixed layer varied between 5 - 15 m with the lowest salinities seen in the Norwegian coastal water mass ( $S < 28$ ) and the highest surface salinities being found above the well mixed shallow parts of the North Sea ( $S \sim 34.5$ ).

A distinct subsurface oxygen maximum ( $O_2 > 240 \mu\text{mol kg}^{-1}$ ) between ~15 - 35 m depth characterised the deeper area north 15 of the shelf-edge whereas a less well-defined maximum was present above the shelf-edge and in the shallow North Sea (Fig. 2c). The bottom water (~20 - 60 m) in the shallow areas exhibited relatively low oxygen concentrations, i.e.,  $< 200 \mu\text{mol kg}^{-1}$ . High nitrate concentrations characterised Atlantic water masses whereas very low nitrate concentrations were observed in the surface layer and above the shallow southern part of the area (Fig. 2d).

### 3.2 Chlorophyll and nutrient distributions

20 The subsurface chlorophyll concentrations were relatively high ( $> 2 \text{ mg chl a m}^{-3}$ ) in the shallower regions of the study area (Fig. 3). A narrow well-defined subsurface chlorophyll maximum extended from the shelf-edge towards the Norwegian coast, i.e. close to the  $27 \text{ kg m}^{-3}$  isopycnal. The depth of the subsurface chlorophyll maximum tracked the nutricline from the shelf-edge, where the nutricline was separating the nutrient-depleted surface layer from the nutrient rich Atlantic water (Fig. 4a, b).

25 In general, a sharp nutricline separated the nutrient depleted surface layer from the nutrient rich Atlantic water with nitrate concentrations above  $6 \mu\text{mol kg}^{-1}$ . For example, an increase from values below the detection limit ( $0.1 \mu\text{mol nitrate kg}^{-1}$ ) to values above  $2 \mu\text{mol kg}^{-1}$  was observed across a 5 m distance (35 - 40 m depth) at the shelf-edge on time series station T2 at Tr4 ( $57.31$  °N). The nutricline between CNSW and AWu was located at density-anomalies of  $\sim 27.3 \text{ kg m}^{-3}$ , whereas the nutricline was located below the  $26.5 \text{ kg m}^{-3}$  isopycnal in areas influenced by SSW and Norwegian coastal water masses. Thus, 30 high nutrient concentrations were found in the cold ( $< 8$  °C) Atlantic water masses and low concentrations were associated with CNSW, SNSW and SSW.

Nitrate was not detectable at the southernmost stations south of 56.88° N at Tr5, 57.00° N at Tr4 and Tr3 and 57.21° N at Tr2, whereas the southernmost station at Tr1 showed detectable nitrate (0.2 - 0.3  $\mu\text{mol kg}^{-1}$  between the surface and 30 m) at the near-coastal station, likely influenced by nutrient-rich JCW (Fig. 1). Bottom samples were typically made down to ~5 m from the bottom, i.e. within the benthic boundary layer, and, considering the relatively large turbulent diffusion coefficients in the benthic boundary layer, this supported the interpretation that no detectable nitrate was present in the water column at the southernmost stations along Tr2-Tr5.

The assumption that nitrate was the limiting nutrient for phytoplankton was supported by the phosphate distributions, in that the N:P-ratio was found to be significantly below Redfield (16:1) at all stations and all depths, with the exception of a few samples above the shallow area (Fig. 4c). Nitrate depletion was observed at stations above the shallow southern North Sea, where excess phosphate compared to the Redfield N:P ratio suggested significant denitrification to be occurring. There was, in general, no indication of silicate limitation because relatively high values (up to 10  $\mu\text{mol kg}^{-1}$ ) were observed above the nitrate-depleted shallow area and low silicate values in the deeper part were also associated with low nitrate concentrations (not shown).

15

### 3.3 Mixing and vertical nitrate fluxes

Dissipation of TKE was low, i.e.,  $< 10^{-9} \text{ W kg}^{-1}$ , below ~40 m in the deeper areas north of the shelf-edge but increased by an order of magnitude above the shelf-edge, where values up to  $\sim 10^{-6} \text{ W kg}^{-1}$  in the benthic boundary layer were recorded (Fig. 5a, b). Dissipation rates of TKE in the 20 – 40 m depth range varied between  $10^{-8} - 10^{-9} \text{ W kg}^{-1}$  above the deeper areas and increased to  $10^{-7} - 10^{-8} \text{ W kg}^{-1}$  above the shallow areas along Tr2. In the upper part of the water column, between 10 - 20 m depth, the dissipation rate of TKE increased to  $10^{-5} - 10^{-7} \text{ W kg}^{-1}$  due to mixing induced by wind and waves. The distribution of the vertical turbulent diffusion coefficient showed a characteristic pattern along all transects where very low  $k_v$ -values of  $< 10^{-6} \text{ m}^2 \text{ s}^{-1}$  between 15 - 30 m depth characterised the deeper open areas, i.e. around the pycnocline. ~~Elevated~~Increased mixing was seen at the shelf-edge and in the ~10 m thick benthic boundary layer further south above the shallow shelf (Fig. 5c,d; note that the shallow turbulence profiles on Tr4 did not resolve the benthic boundary layer). The highest  $k_v$ -values, i.e.,  $> 10^{-4} \text{ m}^2 \text{ s}^{-1}$ , were observed at the shelf edge and in the benthic boundary layer above the shallow part of the shelf.

Vertical nitrate fluxes were calculated for all stations where both nutrients and turbulence profiles were measured. Examples are shown for four stations across the shelf edge on Tr4, obtained 27 July between 14h and 17:30h, with a station spacing of ~5km, in an area where there is a northward increase of the depth from 82 to 122 m (Fig. 6). The nutricline was located at ~35 m and this depth was relatively close to the ~~increased~~elevated mixing in the bottom boundary layer. Increased mixing is seen at the station located at 57.404 °N (Fig. 6c, g) and this results here in a maximum nitrate flux to the euphotic layer of 0.3 mmol

30

$\text{N m}^{-2} \text{d}^{-1}$  at ~40 m. In general, the maximum vertical nitrate flux into the euphotic zone in the deeper parts along the five transects was located 5-10 m below the nutricline (Fig. 3, orange squares). whereas the SCM was located at the nutricline (Figs. 3, 6a). Although the nitrate flux at this depth was relatively low, this showed the close relationship between SCM and nutricline depth.

### 5 3.4 Photosynthetic parameters

Photosynthetic parameters can vary as a function of sampling time and in situ light conditions. Therefore, in order to be able to compare the potential PP at different stations, we averaged photosynthetic parameters for the surface layer (5 m) and from the SCM, respectively. In total, 64 incubations were made. Fifty eight of the incubations were fitted with the photoinhibition term whereas 6 incubations did not show any significant decrease for increasing light levels. Therefore, the inhibition term was excluded in these calculations. To make the data set representative for the whole study area, incubations from the closely spaced (1-3 km) stations on Tr2 were excluded (i.e. 14 stations between the two stations shown with incubations at Tr2 in Fig. 1a) and, to reduce the impact from outliers, representative values are calculated as median and median absolute deviation values (Table 1).

The median chlorophyll concentrations at the surface and SCM were 0.16 and 1.68  $\text{mg chl a m}^{-3}$ , respectively. This reflected the general increase in chlorophyll with depth observed over the entire area. The chlorophyll-normalised photosynthetic parameters of the photosynthetic rate constant ( $P_{\text{max}}^{\text{B}}$ ) and the slope of the PE-curve ( $\alpha^{\text{B}}$ ) in the surface layer were 5.48  $\mu\text{g C } (\mu\text{g Chl h})^{-1}$  and 0.041  $\mu\text{g C } (\mu\text{g Chl h } \mu\text{E m}^{-2} \text{s}^{-1})^{-1}$ , respectively, and the corresponding values of  $P_{\text{max}}^{\text{B}}$  and  $\alpha^{\text{B}}$  at the SCM were 2.33 and 0.027. Thus,  $P_{\text{max}}^{\text{B}}$  was significantly lower at the SCM, in general accordance with previous studies (see review in Richardson et al., 2016) whereas  $\alpha^{\text{B}}$  showed a weak decrease with depth (with overlapping uncertainty intervals between the two depth levels). In general,  $\alpha^{\text{B}}$  has been found to increase significantly with depth (resulting in a more efficient photosynthetic response at low light levels) and inspection of the vertical distribution showed a tendency to higher values between 15 -25 m depth (i.e. 2 - 3 e-folding depth of PAR) and lower values below 30 m resulting in a lower median value from SCM level. It was noted that a similar pattern of  $\alpha^{\text{B}}$ , with a subsurface maximum, has been observed at the European shelf in the Celtic Sea (Hickman et al., 2012).

There was a significant averaged photoinhibition ( $\beta^{\text{B}}$ ) at both depth levels (1.70 and 3.00 ( $10^{-3} \mu\text{g C } (\mu\text{E m}^{-2} \text{s}^{-1} \text{h})^{-1}$ )). However, the average values at these depths were not significantly different. The maximum PP was characterised by  $P_{\text{max}}^{\text{B}*}$ -values of 4.76 and 1.72  $\mu\text{g C } (\mu\text{g Chl h})^{-1}$  at the surface and SCM, respectively, corresponding to maximum PP at PAR-levels of 413 and 192  $\mu\text{E m}^{-2} \text{s}^{-1}$ . The averaged parameters for the two depth levels of  $P_{\text{max}}^{\text{B}}$ ,  $\alpha^{\text{B}}$  and  $\beta^{\text{B}}$  were applied for calculating PP in the water column according to Eq. (3). A comparison was made between the resulting PE-curves and the maximum averaged PP from all the incubations (i.e. the  $P_{\text{max}}^{\text{B}*}$  and  $E_{\text{max}}$  in Table 1). These values were found to fit the averaged curves for the two

depth levels within 5% and, therefore, the PE-curve based values in Table 1 were assumed to be representative of average conditions and applied in the calculation of PP for all of the stations.

### 3.5 Vertically integrated chlorophyll, PP and NP

5 The vertically integrated chlorophyll in the euphotic zone (50 m) showed a local maximum south of the shelf-edge along all transects and a decrease in chlorophyll further south at the two westernmost transects, i.e. Tr4 and Tr5 (Fig. 7a). Relatively low values were observed in the area north of the shelf-edge with the exception of an area close to Norway where high values were observed. The averaged vertically integrated chlorophyll from all stations was  $29.9 \pm 7.8$  mg chl a m<sup>-2</sup> (std. dev., n = 128).

10 The distribution of vertically integrated total PP showed a similar pattern with increased PP-levels south of the shelf edge and a somewhat reduced PP further south at the two westernmost transects (Fig. 7b). A tendency to minimum values was observed at the shelf edge with an increasing tendency towards Norway with high PP-values being observed at a few stations near the Norwegian coast. The averaged vertically integrated PP from all stations was  $476 \pm 110$  mg C m<sup>-2</sup> d<sup>-1</sup> (n=128).

15 The maximum nitrate flux into the euphotic zone ( $F_{NO_3}$ ) and the f-ratio were calculated for each station where nitrate and turbulence measurements were made and where nitrate was present in detectable concentrations. The vertical distribution of the maximum nitrate flux was, in general, characterised by being located below the SCM (cf. Fig. 3, Table 2). However, the horizontal distribution showed a characteristic pattern where increased~~Elevated~~ fluxes and f-ratios were found along the shelf-edge on Tr2-Tr5 (nitrate fluxes were not measured at the shelf edge and at shallow stations at Tr1). Increased fluxes were~~and~~  
20 also observed -near the Norwegian coast at Tr1 and Tr4, and low nitrate fluxes and f-ratios characterised the open area between the shelf edge and Norway (Fig. 7c, d).

### 3.6 Distributions across the shelf-edge

A comparison of distributions of PP related parameters across the shelf-edge showed common trends over all five transects (Fig. 7, S32). Vertically integrated chlorophyll and PP were relatively low, with values of  $\sim 20$  mg chl a m<sup>-2</sup> and  $\sim 400$  mg C m<sup>-2</sup> d<sup>-1</sup>, respectively, on the southernmost parts of the transects. A gradual northward increase towards maximum values (of  $\sim 60$  mg chl m<sup>-2</sup> and  $>1000$  mg C m<sup>-2</sup> d<sup>-1</sup>) was observed within a distance of  $\sim 20$  km south of the shelf edge on Tr3 - Tr5. Transect 2 did not reach as far south of the shelf-edge. This could explain the southern maximum in chlorophyll and PP at Tr2. Transect 1 was influenced by nutrient rich JCW and this may be the reason for the high chlorophyll concentration ( $43$  mg chl a m<sup>-2</sup>) and PP ( $1746$  mg C m<sup>-2</sup> d<sup>-1</sup>) at the southernmost station on this transect.

30

Relatively low values of  $\sim 20 \text{ mg chl m}^{-2}$  and  $400 \text{ mg C m}^{-2} \text{ d}^{-1}$ , respectively, characterised chlorophyll and PP at the shelf-edge zone. These values increased slightly towards Norway to  $\sim 30 \text{ mg chl a m}^{-2}$  and  $5\text{-}600 \text{ mg C m}^{-2} \text{ d}^{-1}$ , respectively. High values were observed in Norwegian coastal water masses on Tr1 and Tr4, probably due to PP being stimulated by coastal upwelling (also indicated by relatively cold Norwegian coastal surface water masses observed from satellite in Fig. 1b). Stations on Tr2 and Tr4 were visited twice within one week. Significant temporal variation of chlorophyll and PP was observed (Fig S32) between samplings. Chlorophyll increased by up to 40% above the shallow area near the shelf edge and a similar increase was seen in PP. Relatively large temporal variations were also seen in these parameters in the coastal Norwegian water masses.

A nutricline could, in general, not be identified above the shallow areas south of the shelf-edge except at two stations on Tr3 and Tr4 (cf. Fig. 2c, d, at both stations high nitrate concentrations of  $0.9 - 1 \text{ } \mu\text{mol kg}^{-1}$  were only measured at 5 m while low values of  $0.1 - 0.3 \text{ } \mu\text{mol kg}^{-1}$  were found below 10 m). The deepest nutricline depths ( $\sim 40 \text{ m}$ ) were found near the shelf-edge. Nutricline depth decreased to  $\sim 20 \text{ m}$  going northwards but then increased again in the coastal Norwegian water masses (Fig 8c). Nitrate fluxes were generally very low ( $< 0.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) in the deeper area north of the shelf edge due to low vertical mixing in the upper 50 m. However, the largest elevated nutrient fluxes of  $-1 \text{ mmol N m}^{-2} \text{ d}^{-1}$  were seen in the shelf edge zone and near the Norwegian coast. This resulted in f-ratios above 0.10 in these regions compared to  $< 0.02$  for the remainder of the study area (Fig. 7, S32).

The distributions were analysed across the shelf edge by dividing the stations into three depth ranges characterising the shallow area (50 - 80 m), the shelf edge zone (80 -130 m) and the deep area ( $> 130 \text{ m}$ ), respectively (Table 2). Although the shelf edge was characterised by the largest nutrient fluxes, the averaged values were not significantly higher than observed above the deeper areas. However, the depth of the maximum flux was found to be significantly deeper ( $\sim 43 \text{ m}$ ) above the shelf edge than in the deeper area ( $\sim 32 \text{ m}$ ). This can be explained by the significantly deeper nutricline at the shelf edge ( $\sim 35 \text{ m}$ ) than observed above the deeper area ( $\sim 27 \text{ m}$ ). Distributions of vertically integrated chlorophyll and PP support that minimum values are found above the shelf edge. However, the low values are not significantly different from the larger values above the deeper and shallower part of the area.

### 3.7 Temporal variability at the shelf edge

Data was collected over 36 hours from a time series station located on the shelf edge on Tr4 (depth 82 m,  $57.314 \text{ }^\circ\text{N}$ ,  $6.765 \text{ }^\circ\text{E}$ , from 29 July 7:07h to 30 July 19:25h) where CTD-casts and turbulence measurements were carried out every hour (although no turbulence measurements were made during the night at this station). Variability was related to the tidal current obtained from the barotropic OTIS model of the North Sea (Egbert and Erofeeva, 2002). The model depth (h) at the time series location was 80 m, it considers eleven tidal constituents, its general performance has previously been validated and a comparison was also made against tide tables for the period from Hanstholm harbor located on the Danish coast ( $57.17 \text{ }^\circ\text{N}$ ,  $8.62 \text{ }^\circ\text{E}$ ). The model result showed excellent agreement with the tidal phases. Tidal energy input was estimated from the cube

of the barotropic tidal current ( $u^3$ , e.g. Simpson and Sharples, 2012). This energy input represents the source for tidally induced vertical mixing and can be compared with turbulent mixing in the water column.

The water column was characterised by a homogenous mixed layer in the upper 5-10 m, a pycnocline at ~20 m, and a relatively homogenous temperature and salinity distribution below ~45 m ( $\theta < 8$  °C) (Fig. 8). A sharp nutricline between 38 - 40 m separated the nitrate-depleted surface layer from the nitrate rich bottom water ( $\sim 2 \mu\text{mol kg}^{-1}$ , not shown). An oxygen maximum layer between 20 - 40 m separated the oxygenated surface layer from the bottom layer with a relatively lower oxygen concentration. Weak temperature and salinity stratification was observed in the start and end of the period (i.e. between DoY 210.3-210.7 and 211.3-211.7) and a corresponding change was observed in the bottom oxygen concentration. The period between DoY 210.6-211.2 was characterised by a relatively homogenous bottom layer ( $< 40$  m). Increased turbulence ( $\epsilon$ ,  $k_v$ ) and decreased stratification ( $N^2$ ) were also observed in this period (Fig. 8d-h). Mixing in the bottom layer increased simultaneously with tidal energy input (Fig. 8a, b). This indicated that tidal barotropic currents overlain on baroclinic currents along the shelf edge could explain the temporal variability in turbulence.

Dissipation of TKE in the bottom layer at the time of the maximum observed dissipation (DoY=210.8) was comparable with the energy input from the tides ( $\sim 10^{-3} \text{ W m}^{-2}$ ). ~~This suggests that~~ A additional energy for turbulence may also be provided from non-tidal currents along the shelf-edge (strong eastward currents below 20 m were noted at the time of some of the turbulence profiles). A relatively large deepening of both T, S and  $\text{O}_2$  below the pycnocline was observed between DoY ~ 211.25-211.4. Nutrient concentrations below 60 m showed an increase from 2 - 3 to 5 - 6  $\mu\text{mol kg}^{-1}$ . This indicated advection of water below the pycnocline could explain the short-term variation observed.

Thus, the observed temporal variability in water column structure and nutrient distributions at the shelf edge shows that varying mixing intensities may interfere with the bottom of the euphotic zone and, thereby, promote diapycnal nutrient fluxes and stimulate NP. The variability arises due to different physical processes, which cannot be identified in detail from the present data set. This may also explain the observed variability between stations located in the shelf edge area (Table 2). Periods of low mixing in the euphotic zone may be followed by short periods of intense mixing. Such temporal variability is a challenge to document over a larger area.

#### 4 Discussion

The shelf edge was identified in this study as a potential area of localised NP during the stratified summer period in the northeastern North Sea. Very low nitrate fluxes and f-ratios were estimated for most of the open water extending northwards from the shelf edge towards Norway. Likewise, little or no NP was estimated to be occurring in the nitrate depleted shallow reaches of the southern North Sea. Previous studies have shown that shelf edge areas can be productive regions, for example

characterised by increased fishing activity (Sharples et al., 2013). In relation to the observations reported by Sharples et al., we speculate that the abundance of fish in this area could be related to a localised increase in NP relative to surrounding waters. It can also be noted that the northeastern shelf edge area is characterised by ~~increased~~~~elevated~~ fish species diversity (ICES, 2008), suggesting that the introduction of new nutrients to the euphotic region of the water column identified for this region may be influencing both food webs and ecosystem structure.

Localised NP at the shelf edge will also influence the oxygen concentration in subsurface water masses (Fig. 2). This can have a direct influence on ambient water with relatively low oxygen above the shallow shelf and influence conditions further downstream, where water masses from the shelf edge eventually reach the North Sea/Baltic Sea transition zone and contribute to bottom water ventilation in more eutrophic areas (Bendtsen et al., 2009).

The possible occurrence of localised NP also implies that physical processes on relatively small spatial scales (~1 km) are important for modelling NP in the area. This is in general accordance with model studies where the resolution of physical processes at high spatial scales was found to be necessary to explain observed patterns of PP in the North Sea (Skogen and Moll, 2000). Holt et al. (2012) applied a high-resolution model of the whole North Sea area and showed that nutrient transports towards the shelf area were of primary importance for understanding PP and also for assessing the impact from climate change. Localised NP at the shelf edge in the northeastern North Sea may be representative for the open ocean - shallow shelf exchange of nutrients more generally. If so, then this NP may also impact nutrient conditions above the shallow central North Sea and may explain some of the recent decadal decline of PP in this area (Capuzzo et al., 2018).

#### 4.1 Regenerated production above the shallow shelf

There was no measurable nitrate in the water column at stations south of the shelf-edge., i.e. an area where the whole water column was within the euphotic zone, i.e. < 50 m (Fig. 1a, yellow lines). This indicates that nitrate sinks, i.e. biological consumption or denitrification, exceed nitrate sources, i.e. nitrification, nitrogen-fixation or advective supply during summer months in this region. Significant nitrification may take place in the water column (Clark et al. 2008; Zehr and Kudela, 2011) or in the sediment and, as pointed out in the work of Dugdale and Goering (1967), nitrate can, in this case, not be considered as a non-regenerated nutrient form in the euphotic zone. Yool et al. (2007) estimated a global specific nitrification rate of 0.2 d<sup>-1</sup>, thus, even small concentrations of ammonium could lead to significant nitrification rates. Concentrations of ammonium were, however, very low in the nitrate depleted area. For example, ammonium was undetectable at all nitrate-depleted stations on Tr5 and this indicated a relatively small contribution from nitrification in the euphotic zone. Observed nitrification rates span a large range (Yool et al., 2007) and the importance of nitrification varies between ocean regions (Clark et al, 2008;

Fawcett et al., 2015). Therefore, it remains an open question whether or not significant nitrification takes place in the euphotic zone in the area.

5 Diazotrophy constitutes another potential source of nitrogen to the nitrate-depleted surface layer and  $N_2$ -fixation has been measured in the southern North Sea at Dogger Bank (Fan et al., 2015). However, the estimated nitrogen fluxes from  $N_2$ -fixation were very small compared to the relatively high PP. Increased nutrient fluxes and NP at the shelf-edge could also support PP in the ambient shallow areas through isopycnal transport of dissolved organic material. A substantial fraction of dissolved organic material remineralises on time-scales of days to weeks (Bendtsen et al., 2015; Hansen and Bendtsen, 2014) and isopycnal transport of organic matter could then supply organic nitrogen from the shelf edge zone. Both the nitrification and  
10 isopycnal supply of organic material, thus, potentially provide new nitrogen to the shallow area and this confuses the concept of nitrate-based new versus regenerated production here. However, nitrification in the euphotic zone would be based on regenerated production and, therefore, we consider PP to be regenerated production in areas without detectable nitrate in the water column.

15 Recycling of organic matter above the shallow shelf could, thus, be maintained by regenerated organic matter in the water column or sediment and we analysed whether this was in accordance with estimated carbon and nitrogen pools. The high biomass in the shallow area, indicated by chlorophyll concentrations of  $\sim 2 - 4 \text{ mg chl m}^{-3}$  in the bottom layer, would rapidly consume a regenerated pool of inorganic nitrogen. The regenerated cycling could, in principle, originate from the winter concentration of nitrate of  $\sim 6 \text{ mmol DIN m}^{-3}$  in the area (Pätk and Kühn, 2008). The nitrate distribution in the shallow area  
20 indicates a large denitrification ranging within  $0 - 4 \text{ mmol DIN m}^{-3}$  (Fig. 4c), and this would correspond to a pool of more than  $\sim 2 \text{ mmol DIN m}^{-3}$  available for establishing the phytoplankton biomass. Denitrification rates in the sediment of  $0.02 - 0.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$  have been observed at the Dogger Bank between May and August (Fan et al., 2015) and such high rates could explain the indicated nitrate sink. Assuming a Redfield C:N molar ratio of 6.6 and a C:chlorophyll ratio of  $1 \text{ mg C}/50 \text{ mg chl}$ , this would equal  $\sim 3 \text{ mg chl m}^{-3}$ , i.e., in general accordance with the observed concentrations of  $<1$  and  $\sim 4 \text{ mg chl m}^{-3}$  in the  
25 surface and bottom layers, respectively. Relatively low oxygen concentrations in the bottom layer also suggested an active bacterial respiration (Fig. 2c) to be occurring here. Thus, regenerated production could be maintained and explained by recycling of an initial nutrient pool from early spring.

#### 4.2 Photosynthetic parameters and PP

30 Estimates of PP based on photosynthetic parameters from  $^{14}\text{C}$ -incubations and in situ conditions of light and chlorophyll rely on several critical assumptions, including the values used for photosynthetic parameters, the distribution of chlorophyll, light conditions and nutrient-carbon relationships. Photosynthetic parameters from individual incubation experiments were well described by the PP-model (i.e. PP described by the terms in the integrals in Eq. (3), where parameter values are taken from

incubations, see Fig. S2 for examples of incubation data) so uncertainty is mainly related to the spatial and temporal variability of these parameters. Photosynthetic parameters are bulk parameters describing the physiological response of the phytoplankton community as a whole to a given a photon flux. Thus, both algae composition and actual fitness of the cells contribute to the observed range of these parameters.

5

The photosynthetic parameters represent the conditions of the phytoplankton community at the time of sampling. However, these may vary during the day (Richardson et al., 2017) or during different light conditions (e.g., photo-inhibition). Thus, PP-calculations based on spatial and temporal averaging of the photosynthetic parameters from the surface and SCM (cf. Table 1) may result in a more representative PP than obtained from photosynthetic parameters obtained from a single PP-incubation.

10

The values reported here (Table 1) for photosynthetic parameters are comparable with those found in previous studies in the North Sea (e.g. Weston et al., 2005). Variability of the photosynthetic parameters, e.g. the uncertainty of the surface value of  $P_{\max}^B$  of  $\sim\pm 30\%$ , implies a corresponding uncertainty in PP. Thus, using a common set of photosynthetic parameters implies an uncertainty-even within this relatively small study area, and similar limitations would probably apply to other PP estimates for the North Sea area. These considerations illustrate that a better understanding of the distributions of photosynthetic parameters and the factors underlying these distributions is a prerequisite for improved estimates of PP on regional and larger scales. Given the uncertainties related to the determination of the absolute rate of PP at individual stations, we believe the most robust manner by which to compare PP and NP over our study area is to use constant (average) values for photosynthetic parameters for all stations.

20

#### 4.3 Nutrient fluxes and NP at the shelf edge zone

The largest vertical nitrate fluxes of up to  $>0.5$   ~~$-1.5$~~  mmol N m<sup>-2</sup> d<sup>-1</sup> were restricted to the area above the shelf edge where increased mixing in the bottom layer intersected the nutricline within the euphotic zone. ~~Similar to~~ Large nitrate fluxes have been observed along the European shelf where tidally induced (Sharpley et al., 2001; located in the English Channel) or wind-induced mixing (Williams et al., 2013; Celtic Sea) leads to daily averaged vertical fluxes of 1 - 2 mmol N m<sup>-2</sup> d<sup>-1</sup>. Significantly larger fluxes have also been observed above steep bathymetric gradients (Tweddle et al., 2013). Wind and tidal mixing may also provide energy for intensified mixing along the northeastern shelf edge in the North Sea, although the present study did not resolve the specific cause for increased mixing. Shelf-edge zones are dynamic areas where cross-shelf exchange may occur due to many different dynamic processes (Huthnance, 1995; Brink, 2012).

30

Mixing associated with wind and tides (e.g. Burchard and Rippeth, 2009) as well as breaking internal waves (Sharples et al, 2007; 2009) has been shown to be important for vertical nutrient fluxes in shelf areas. The specific physical processes behind increased turbulent mixing cannot be identified from the present data set. Measurements on the time series station at the shelf edge showed that ~~increased~~ ~~elevated~~ mixing occurred in phase with the tidal energy input but also that additional energy sources likely contributed to the ~~increased~~ ~~elevated~~ mixing, e.g. energy from non-tidal currents. Short term variability associated with advection of ambient water masses was also observed. This could possibly be related to sub-mesoscale eddies or other transport processes occurring below the pycnocline. The time series station T2 at Tr4 showed an important feature where mixing associated with the bottom boundary layer increased and intersected the bottom of the euphotic zone. Thus, the combined effect from a deep nutricline and ~~increased~~ ~~elevated~~ mixing provide a mechanism for increased diapycnal nutrient fluxes along the shelf edge.

Other processes may be important on the northeastern shelf edge due to the large in- and outflow of Atlantic water masses. It is interesting to note that the deepening of the nutricline from the open areas towards the shelf edge mirrors the slope of the pycnocline. The slope of the pycnocline implies, via the thermal wind equations, an increased eastward baroclinic velocity component with depth, in accordance with the general cyclonic circulation in the area. Thus, deepening of the nutricline can potentially be explained as a dynamic response to a shelf-edge current transporting Atlantic water into the area.

The conditions across the shelf edge observed during the stratified summer season may, therefore, be considered as a stable quasi-stationary system where mixing at the shelf edge, associated with a deep nutricline and nutrient rich bottom currents, provide nutrients to the euphotic zone stimulating localised new production in this area (Fig. 9). Isopycnal mixing may provide organic matter for increased regenerated production above the nitrate-depleted shallow shelf area and also, together with upwelling along the Norwegian coast, provide fresh organic material to the euphotic zone off the shelf edge towards Norway. Thus, the tendency towards increased chlorophyll concentrations and PP on either side of the shelf edge might be explained as being a result of the gradual build-up of biomass as nutrients are transported away from the shelf-edge region by isopycnal mixing. Alternatively, the tendency to low values above the shelf edge could also be explained by a larger grazing pressure above the shelf edge. Thus, a full explanation of the tendency to low chlorophyll and PP above the shelf edge area cannot be determined from these data.

#### 4.4 Vertical nutrient fluxes in the euphotic zone

The position of the SCM was closely related to the depth of the nutricline (e.g. Fig. 3 and 6) and located in the middle of the euphotic zone (average nutricline depth from all stations was  $29.1 \pm 9.7$  m,  $n = 83$ ). The maximum nitrate flux was found at depth levels between 3.4 m above and 23.1 m below the nutricline. However, on average, it was located  $6.4 \pm 7.7$  m ( $n=73$ )

below the nutricline depth (e.g., Fig. 6). Thus, the maximum nitrate flux was, ~~in general~~, within the euphotic zone but, in general, significantly below the SCM (Fig. 3). This implies that internal recycling from below the SCM towards the surface of regenerated nitrogen is necessary for maintaining the phytoplankton biomass in the upper layer. Considering the relatively low vertical mixing rates around the SCM (e.g., a turbulent diffusion coefficient of  $<5 \cdot 10^{-5} \text{ m}^2 \text{ s}^{-1}$  implies a time scale of  $\sim 3$  weeks for mixing across a 10 m thick layer, Fig. 5), this indicates that other transport processes within the euphotic zone are important in this area. One possible mechanism could be diel vertical migration of plankton. Raven and Richardson (1984) showed the potential for diel vertical migration as an efficient strategy for phytoplankton to get access to both nutrients and light. Such a strategy might be particularly beneficial for phytoplankton in the low-mixing zone in the pycnocline north of the shelf edge (e.g., Fig. 5d at  $\sim 20$  m depth north of  $57.4^\circ\text{N}$ ), where the vertical diffusion coefficient is below  $5 \cdot 10^{-5} \text{ m}^2 \text{ s}^{-1}$  in a  $\sim 20$  m deep layer. Applying a typical swimming speed for some dinophytes of  $\sim 10 \text{ m day}^{-1}$  across a 10 m deep layer in such a region implies a Peclet number  $\gg 1$ , thus, diel vertical migration is a potential additional nitrogen transport although this cannot be documented from our data.

#### 4.5 Nutrient fluxes north of the shelf edge

Nutrient fluxes and NP increased close to the Norwegian coast (Fig. 7, S32). This was in accordance with chlorophyll estimates (Hu et al., 2012) based on daily images from the MODIS-Aqua satellite: A large algal bloom was observed 6 July (not shown) and covered the area off the southern-most part of Norway. A satellite image from 20 July (Fig. 1a) showed increased chlorophyll concentrations near the Norwegian coast and colder sea surface temperatures along the coast also indicated influence from upwelling of subsurface water masses (Fig. 1b). Although our observations were made more than 12 nautical miles from the coast, the ~~increased~~elevated chlorophyll and PP values at Tr1 and Tr4 are likely related to these features. A tendency to a thicker chlorophyll layer around the SCM and a deeper nutricline at Tr4 and Tr5 also indicates increased production and supply of nutrients near the coast. Mixing processes along the Norwegian shelf edge may, therefore, similarly contribute to NP in the area.

#### 5 Conclusions

Relatively high PP and chlorophyll concentrations of  $476 \text{ mg C m}^{-2} \text{ d}^{-1}$  and  $30 \text{ mg chlorophyll m}^{-2}$ , respectively, characterised the stratified northeastern North Sea in July 2016. The greatest values were found above the shallow shelf and near the Norwegian coast. Turbulence measurements showed maximum dissipation rates of TKE in the benthic boundary layer above the shallow shelf area and ~~increased~~elevated mixing above the shelf edge zone, whereas very low vertical mixing rates characterised the deeper open area. Chlorophyll was concentrated in a subsurface chlorophyll maximum located near the nutricline and, on average, about 6 m above the depth of the maximum vertical nitrate flux in the deeper area north of the shelf edge. Chlorophyll was concentrated in the bottom layer above the shallow and nitrate depleted shelf area. The nutricline was

located significantly deeper above the shelf edge area (depth ~80 - 130 m) than in deeper water columns. Significant NP was found above the shelf-edge ~~where, at some stations, relatively large nitrate fluxes, i.e. >where vertical nitrate fluxes of 0.5–1.5~~ mmol N m<sup>-2</sup> d<sup>-1</sup> implied f-ratios above 0.10. ~~In contrast, whereas~~ very low nutrient fluxes characterised the open area above the Norwegian Trench (f-ratios < 0.02). This localised NP along the shelf edge potentially represents an important key to understanding temporal variability in the distribution of organisms (diversity), biological production, and ecosystem structure in this productive area.

### Author contribution

Measurements of primary production and turbulence were carried out by KR and JB, respectively, and both analysed the data and prepared the manuscript.

### Acknowledgements

We thank captain and crew on-board R/V Dana for very helpful assistance and support during the cruise and Eik Ehlert Britch for technical support. Erik Askov Mousing carried out most of the PP incubations. This study was supported by funding for ship-time by the Danish Centre for Marine Research. The Carlsberg foundation provided support for the turbulence instrument (CF15-0301). The Villum foundation provided support for the cruise and analysis of the measurements. Analyses were supported by Danish National Science Foundation via its support of the Center for Macroecology, Evolution, and Climate (grant no. DNRF96). Satellite derived PAR-data was obtained from NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group (2014): MODIS-Aqua Ocean Color Data, <http://doi.org/10.5067/AQUA/MODIS/L3M/PAR/2018> and <http://doi.org/10.5067/AQUA/MODIS/L3M/CHL/2018>, (Accessed on 2018/05/10). [The manuscript benefitted from comments by two anonymous reviewers.](#)

### References

- Bendtsen, J., Gustafsson, K. E., Söderkvist, J., and Hansen, J. L. S.: Ventilation of bottom water in the North Sea – Baltic Sea transition zone, *J. Mar. Sys.*, 75, 138–149, doi: 10.1016/j.jmarsys.2008.08.006, 2009.
- Bendtsen, J., Hilligsøe, K. M., Hansen, J. L. S., and Richardson K.: Analysis of remineralisation, lability, temperature sensitivity and structural composition of organic matter from the upper ocean, *Prog. Oceanogr.*, 130, 125–145, doi: 10.1016/j.pocean.2014.10.00, 2015.
- Bouffard, D., and Boegman, L.: A diapycnal diffusivity model for stratified environmental flows, *Dyn. Atmos. Oceans*, 61-62, 14–34, doi:10.106/j.dynatmoce.2013.02.002, 2013.

- Brink, K. H.: Cross-shelf exchange, *Annu. Rev. Mar. Sci.*, 8, 59–78, doi: 10.1146/annurev-marine-010814-015717, 2012.
- Burchard, H. and Rippeth, T.: Generation of bulk shear spikes in shallow stratified tidal seas, *J. Phys. Oceanogr.*, 39, 969–985, 2009.
- Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S. M., Engelhard, G. H.: A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment, *Glob. Change Biol.*, 24, e352–e364, doi: 10.1111/gcb.1391, 2018.
- Clark, D. R., Rees, A. P., and Joint, I.: Ammonium regeneration and nitrification rates in the oligotrophic Atlantic Ocean: Implications for new production estimates, *Limnol. Oceanogr.*, 53, 52–62, 2008.
- Danielssen, D. S., Edler, L., Fonselius, S., Hernroth, L., Ostrowski, M., Svendsen, E., and Talpsepp, L.: Oceanographic variability in the Skagerrak and Northern Kattegat, May–June, 1990. *ICES J. Mar. Sci.*, 54, 753–773, 1997.
- Dugdale, R. C., and Goering, J. J.: Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.*, 12, 196–206, 1967.
- Egbert, Gary D., and Erofeeva, S. Y.: Efficient inverse modeling of barotropic ocean tides, *J. Atm. Ocean. Tech.*, 19, 183–204, 2002.
- Eppley, R. W., and Peterson, B. J.: Particulate organic matter flux and planktonic new production in the deep ocean, *Nature*, 282, 677–680, 1979.
- Fan, H., Bolhuis, H., and Stal, J.: Drivers of the dynamics of diazotrophs and denitrifiers in North Sea bottom waters and sediments, *Front. Microbiol.*, 6, 738, doi: 10.3389/fmicb.2015.00738, 2015.
- Fawcett, S. E., Ward, B. B., Lomas, M. W., and Sigman, D. M.: Vertical decoupling of nitrate assimilation and nitrification in the Sargasso Sea, *Deep-Sea Res. I*, 103, 64–72, 2015.
- Fernand, L., Weston, K., Morris, T., Greenwood, N., Brown, J. and Jickells, T.: The contribution of the deep chlorophyll maximum to primary production in a seasonally stratified shelf sea, the North Sea, *Biogeochemistry*, 113, 153–166, doi: 10.1007/s10533-013-9831-7, 2013.
- From, N., Richardson, K., Mousing, E.A. and Jensen, P.E.: Removing the light history signal from normalized variable fluorescence (Fv/Fm) measurements on marine phytoplankton, *Limnol. Oceanogr.-Meth.*, 12, 776–783, 2014.
- Frouin, R., McPherson, J., Ueyoshi, K., and Franz, B. A.: A time series of photosynthetically available radiation at the ocean surface from SeaWiFS and MODIS data, *Remote Sensing of the Marine Environment II*. doi: 10.1117/12.981264, 2012.
- Gattuso, J.-P., Frankignoulle, M., and Wollast, R.: Carbon and carbonate metabolism in coastal aquatic ecosystems, *Annual Reviews of Ecological Systems*, 29, 405–434, 1998.
- Grasshoff, K., Erhardt, M., and Kremling, K.: *Methods of seawater analysis*, 2. Revision. Verlag Chemie, Weinheim, 1983.
- Hansen, J. L. S., and Bendtsen, J.: Seasonal bottom water respiration in the North Sea–Baltic Sea transition zone: rates, temperature sensitivity and sources of organic material, *Mar. Ecol.-Prog. Ser.*, 499, 19–34, 2014.

- Hickman, A. E., Moore, C. M., Sharples, J., Lucas, M. I., Tilstone, G. H., Krivtsov, V., Holligan, P. M.: Primary production and nitrate uptake within the seasonal thermocline of a stratified shelf sea, *Mar. Ecol.-Prog. Ser.*, 463, 39–57, 2012.
- Holt, J., and Proctor, R.: The seasonal circulation and volume transport on the northwest European continental shelf: A fine-resolution model study, *J. Geophys. Res.*, 113, C06021, doi: 10.1029/2006JC004034, 2008.
- 5 Holt, J., Wakelin, S., Lowe, J., and Tinker, J.: The potential impacts of climate change on the hydrography of the northwest European continental shelf, *Prog. Oceanogr.*, 86, 361–379, 2010.
- Holt, J., Butenschön, M., Wakelin, S. L., Artioli, Y., and Allen, J. I.: Oceanic controls on the primary production of the northwest European continental shelf: model experiments under recent past conditions and a potential future scenario, *Biogeosciences*, 9, 97–117, doi: 10.5194/bg-9-97-2012, 2012.
- 10 Hu, C., Lee, Z., and Franz, B. A.: Chlorophyll-a algorithms for oligotrophic oceans: A novel approach based on three-band reflectance difference, *J. Geophys. Res.* 117, C01011, doi: 10.1029/2011JC007395, 2012.
- Huthnance, J. M.: Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge, *Prog. Oceanogr.* 35, 353–431, 1995.
- ICES: Report of the ICES Advisory Committee 2008. Book 6: North Sea. International Council for the Exploration of the Sea  
15 (ICES), 2008.
- IOC, SCOR and IAPSO: The international thermodynamic equation of seawater – 2010: Calculation and use of thermodynamic properties. Intergovernmental Oceanographic Commission, Manuals and Guides No. 56, UNESCO (English), 196pp, 2010.
- Kumari, B.: Comparison of high performance liquid chromatography and fluorometri ocean colour pigments, *J. Indian Soc. Remot.*, 33, 2005.
- 20 Lueck, R.: Calculating the rate of dissipation of turbulent kinetic energy, RSI Technical Note 028, Rockland Scientific International, Victoria, Canada, 18 pp, 2016.
- McKee, D., Röttgers, R., Neukermans, G., Calzado, V. S., Trees, C., Ampolo-Rella, M., Neil, C., and Cunningham, A.: Impact of measurement uncertainties on determination of chlorophyll-specific absorption coefficient for marine phytoplankton, *J. Geophys. Res. Oceans*, 119-925, 9013–9025, doi:10.1002/2014/JC009909, 2014.
- 25 Osborn, T. R., Estimate of the local rate of vertical diffusion from dissipation measurements, *J. Phys. Oceanogr.*, 10, 83–89, 1980.
- Pätsch, J. and Kühn, W.: Nitrogen and carbon cycling in the North Sea and exchange with the North Atlantic – A model study. Part I. Nitrogen budget and fluxes, *Cont. Shelf Res.*, 28, 767–787, 2008.
- Pätsch, J., Burchard, H., Dieterich, C., Gräwe, U., Gröger, M., Mathis, M., Kapitza, H., Bersch, M., Moll, A., Pohlmann, T.,  
30 Su, J., Ho-Hagemann, Ha T. M., Schulz, A. Elizalde, A., and Eden, C.: An evaluation of the North Sea circulation in global and regional models relevant for ecosystem simulations, *Ocean Model.*, 116, 70–95, 2017.
- Platt, T., Gallegos, C. L., and Harrison, W. G.: Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton, *J. Mar. Res.* 38, 687–701, 1980.

- Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P.: Numerical Recipes in FORTRAN: The Art of Scientific Computing, Press Syndicate of the University of Cambridge, USA, 1986.
- Raven, J. A. and Richardson, K.: Dinophyte flagella: a cost-benefit analysis, *New Phytol.*, 98, 259–276, 1984.
- Redfield, A. C., Ketchum, B. H., Richards, F. A.: The influence of organisms on the composition of sea water. In: Hill, M. N. (Ed.), *The Sea*. Wiley-Interscience, New York, pp. 26–77, 1963.
- Richardson, K., Visser, A.W., and Pedersen, F. B.: Subsurface phytoplankton blooms fuel pelagic production in the North Sea, *J. Plankton Res.*, 22, 1663–1671, 2000.
- Richardson, K., Bendtsen, J., Kragh, T., and Mousing, E. A.: Constraining the distribution of photosynthetic parameters in the global ocean, *Front. Mar. Sci.*, 3, 269, doi: 10.3389/fmars.2016.00269, 2016.
- 10 Røed, L. P., and Fossum, I.: Mean and eddy motion in the Skagerrak/northern North Sea: insight from a numerical model, *Ocean Dynam.*, 54, 197–220, doi:10.1007/s10236-003-0076-1, 2004.
- Scott, B. E., Sharples, J., Ross, O. N., Wang, J., Pierce, G. J. and Camphuysen, C. J.: Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll, *Mar. Ecol.-Prog. Ser.*, 408, 207–226, doi: 10.3354/meps08552, 2010.
- 15 Sharples, J., Moore, C. M., Rippeth, T. P., Holligan, P. M., Hydes, D. J., Fisher, N. R., and Simpson, J. H.: Phytoplankton distribution and survival in the thermocline, *Limnol. Oceanogr.*, 46, 486–496, 2001.
- Sharples, J., Tweddle, J. F., Green, J. A. M., Palmer, M. R., Kim, Y.-N., Hickman, A. E., Holligan, P. M., Moore, C. M., Rippeth, T. P., Simpson, J. H., and Krivtsov, V.: Spring-Neap Modulation of Internal Tide Mixing and Vertical Nitrate Fluxes at a Shelf Edge in Summer, *Limnol. Oceanogr.*, 52, 1735–1747, 2007.
- 20 Sharples, J., Moore, C. M., Hickman, A. E., Holligan, P. M., Tweddle, J. F., Palmer, M. R., and Simpson, J. H.: Internal tidal mixing as a control on continental margin ecosystems, *Geophys. Res. Lett.*, 36, L23603, doi:10.1029/2009GL040683, 2009.
- Sharples, J., Ellis, J. R., Nolan, G., and Scott, B. E.: Fishing and the oceanography of a stratified shelf sea, *Progr. Oceanogr.*, 117, 130–139, 2013.
- Shih, L. H., Koseff, J. R., Ivey, G. N. and Ferziger, J. H.: Parameterization of turbulent fluxes and scales using homogeneous sheared stably stratified turbulence simulations, *J. Fluid. Mech.*, 525, 193–214, doi:10.1017/S0022112004002587, 2005.
- 25 Simpson, J., and Sharples, J.: Introduction to the physical and biological oceanography of shelf seas. Cambridge: Cambridge University Press, 424 pp., 2012.
- Skogen, M. D., and Moll, A.: Interannual variability of the North Sea primary production: comparison from two model studies, *Cont. Shelf Res.*, 20, 129–151, 2000.
- 30 Tweddle, J. F., Sharples, J., Palmer, M. R., Davidson, K., and McNeill, S.: Enhanced nutrient fluxes at the shelf sea seasonal thermocline caused by stratified flow over a bank, *Progr. Oceanogr.*, 117, 37–47, 2013.
- Volk, T., and Hoffert, M.I.: Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO<sub>2</sub>, In: *The Carbon Cycle and Atmospheric CO<sub>2</sub>: Natural Variations Archean to Present*, Geophysical Monograph Series, vol. 32. Sundquist, E.T., Broecker, W.S. (Ed.), AGU, Washington, DC, pp. 99–110, 1985.

Webb, W. L., Newton, M., and Starr, D.: Carbon dioxide exchange of *Alnus rubra*. A mathematical model, *Oecologia*, 17, 281–291, 1974.

Weston, K., Fernand, L., Mills, D. K., Delahunty, R. and Brown, J.: Primary production in the deep chlorophyll maximum of the central North Sea, *J. Plankt. Res.*, 27, 909–922, 2005.

5 Williams, C., Sharples, J., Mahaffey, C., and Rippeth, T.: Wind-driven nutrient pulses to the subsurface chlorophyll maximum in seasonally stratified shelf seas, *Geophys. Res. Lett.*, 40, 5467–5472, doi:10.1002/2013GL058171, 2013.

Winther, N. G., and Johannessen, J. A.: North Sea circulation: Atlantic inflow and its destination, *J. Geophys. Res.*, 111, C12018, doi:10.1029/2005JC003310, 2006.

Wolk, F., Yamazaki, H., Seuront, L., and Lueck, R. G.: A new free-fall profiler for measuring bio-physical microstructure, *J.*  
10 *Atmos. Ocean. Tech.*, 19, 780–793, 2002.

Yool, A., Martin, A. P., Fernández, C., and Clark, D. R.: The significance of nitrification for oceanic new production. *Nature*, 447, 999–1002, 2007.

Zehr, J. P., and Kudela, R. M.: Nitrogen cycle of the open ocean: From genes to ecosystems, *Ann. Rev. Mar. Sci.*, 3, 197–225, 2011.

15

**Figure 1** VERMIX station map of the five transects in the northeastern North Sea overlain on (a) surface chlorophyll a ( $\text{mg chl m}^{-3}$ ) and (b) sea surface temperature ( $^{\circ}\text{C}$ ) from MODIS satellite images (4 km resolution) obtained 20 July 2016 (clouds are shown in dark gray). (a) CTD stations (bullets) and stations where  $^{14}\text{C}$ -incubations for primary production were used for  
20 estimating photosynthetic parameters in the area (white circles) along the five transects (Tr1-5). Horizontal yellow bars (Tr2-5) show the separation between nitrate-deplete and nitrate-replete areas. Water masses in the area are indicated (see text). Bathymetry is contoured in meters.

**Figure 2** Distributions along Tr4 of (a) potential temperature ( $^{\circ}\text{C}$ , colours and white contours, additional contours above 16  
25  $^{\circ}\text{C}$  in 0.5  $^{\circ}\text{C}$  intervals), (b) salinity (psu, colours and white contours, additional contours between 26-34 in 0.5 psu intervals) and contours of potential density anomalies (intervals of 1  $\text{kg m}^{-3}$ , orange lines), (c) oxygen ( $\mu\text{mol kg}^{-1}$ , colours and black contours) and (d) nitrate ( $\mu\text{mol kg}^{-1}$ , colours and white contours and orange contours of potential density anomalies as in b). Vertical lines show location of the CTD-measurements.

**Figure 3** Distributions of chlorophyll a ( $\text{mg chl m}^{-3}$ , colours and black contours, additional white contours are shown in  
30 intervals of 2  $\text{mg chl m}^{-3}$ ) along Tr1-Tr5 (a-e). Nutricline depths (red bullets) and depths with maximum nitrate flux into the euphotic zone (orange squares) were calculated at each station where water samples (black triangles) and turbulence profiles were made, respectively. Contours of potential density anomalies are shown in intervals of 1  $\text{kg m}^{-3}$  (orange lines). Note the different latitude-intervals in the figures.

**Figure 4** (a) Potential temperature-salinity diagram of all CTD-measurements and (b) a high-saline subset of the measurements (small grey bullets). Water sample concentrations of nitrate are shown with large bullets in (a,b) ( $\mu\text{mol kg}^{-1}$ , colour bar).

Contour lines show isopycnals of potential density anomalies and selected water masses are indicated. (c) Nitrate vs phosphate for all water samples. The total water depth is shown with colours (m) and the relationship  $[\text{NO}_3^-] = \eta_{\text{N:P}} [\text{PO}_4^-]$ ,  $\eta_{\text{N:P}} = 16:1$ , is shown with a grey dashed line.

5 **Figure 5** Turbulence measurements along Tr2 (a,c) and Tr4 (b,d). (a,b) Logarithm ( $\text{Log}_{10}$ ) of dissipation of turbulent kinetic energy ( $\text{W kg}^{-1}$ ) and (c,d) calculated vertical turbulent diffusion coefficient ( $\text{m}^2 \text{s}^{-1}$ ).

10 **Figure 6** Vertical profiles from four stations across the shelf edge of (upper panels) potential density anomaly, chlorophyll a and nitrate (bullets) and (lower panels) dissipation of TKE (average value and values from the two shear sensors are shown with bullets and open circles, respectively), Brunt-Väisälä frequency (dashed line), turbulent diffusion coefficient and the vertical turbulent nitrate flux. The nutricline depth ( $D_{\text{NO}_3}$ ) and depth of the euphotic zone (0.1% PAR) are shown (dashed and dotted lines) and station information of locations,  $D_{\text{NO}_3}$  and maximum  $F_{\text{NO}_3}$  to the euphotic zone are ~~shown~~ summarized in the ~~figures~~ tables (e-h).

15 **Figure 7** (a) Vertically integrated chlorophyll a ( $\text{mg chl a m}^{-2}$ ) and (b) primary production ( $\text{mg C m}^{-2} \text{d}^{-1}$ ). Values are proportional to the diameter of the circles. (c) Distribution of maximum nitrate flux to the euphotic zone ( $F_{\text{NO}_3}$ ,  $\text{mmol N m}^{-2} \text{d}^{-1}$ ) and (e) f-ratios for the euphotic zone (colours, no unit).

20 **Figure 8** Time series station over 36h at the shelf edge. (a,b) Tidal current speed cubed, ctd-measurements (c, e, g, h) of potential temperature, salinity, oxygen and Brunt Väisälä frequency, respectively. Turbulence measurements of (d) dissipation rate of TKE and (f) calculated vertical turbulent diffusion coefficient. Observations are shown with small gray bullets and samples for water chemistry is shown with bullets in (g)s.

25 **Figure 9** Sketch of conditions across the shelf edge zone during summer. The largest f-ratios are found above the shelf-edge zone where the nutricline ( $D_{\text{NO}_3}$ ) gets in contact with ~~increased~~ ~~elevated~~ mixing near the bottom. Deep waters are characterized by high nitrate concentration whereas surface water and water above the shallow North Sea (NS) are nitrate depleted.

**Table 1.** Distribution of photosynthetic parameters. Median values, and absolute median deviations (number of samples  $n$  in parenthesis) of photosynthetic parameters at 5 m below the surface and at the SCM.

| Depth level | Depth          | $P_{max}^B$ *                               | $P_{max}^B$                                 | $\alpha^B$  | $\beta^B$  | $E_{max}$                                       | Chl a                    |
|-------------|----------------|---|---|---|--|---|--------------------------|
|             | [m]            | $[\mu\text{g C } (\mu\text{g chl h})^{-1}]$ | $[\mu\text{g C } (\mu\text{g chl h})^{-1}]$ | $10^{-2} \cdot [\mu\text{g C} \cdot (\mu\text{g chl h } \mu\text{E m}^{-2} \text{ s}^{-1})^{-1}]$ | $10^{-3} \cdot [\mu\text{g C } (\mu\text{g chl h } \mu\text{E m}^{-2} \text{ s}^{-1})^{-1}]$ | $[\mu\text{E m}^{-2} \text{ s}^{-1} \text{ h}]$ | $[\text{mg chl m}^{-3}]$ |
| Surface     | 5.0± 0.0 (23)  | 4.76 ± 1.33 (19)                            | 5.48 ± 0.87 (23)                            | 4.10 ± 0.90 (23)  | 1.70 ± 1.70 (23)   | 413 ± 76 (19)                                   | 0.16 ± 0.06 (23)         |
| SCME        | 27.0± 5.0 (25) | 1.72 ± 0.38 (24)                            | 2.33 ± 0.64 (25)                            | 2.70 ± 0.80 (25)  | 3.00 ± 0.90 (25)   | 192 ± 26 (24)                                   | 1.67 ± 0.73 (25)         |

**Table 2** Median values, and absolute median deviations of all data in three depth intervals ~~of depth~~, depth of maximum nitrate flux ( $Depth_{max}$ ), maximum nitrate flux into the euphotic zone ( $FNO3_{max}$ ), depth of nutricline ( $D_{NO3}$ ), vertically integrated chlorophyll a ( $Chl_{int}$ ) and primary production (PP).

| Depth interval (m) | Depth (m)   | $Depth_{max}$ (m) | $FNO3_{max}$ ( $\text{mmol N m}^{-2} \text{ d}^{-1}$ ) | $D_{NO3}$ (m) | $Chl_{int}$ ( $\text{mg chl-a m}^{-2}$ ) | PP ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) |
|--------------------|-------------|-------------------|--|---------------|--|--|
| 50 - 80            | 65±6 (25)   | 39±3 (25)         | 0.05±0.04 (25)   | 34.5±4.5 (28) | 34.8±13.3 (69)                           | 476±138 (69)                               |
| 80 - 130           | 97±11 (18)  | 43±3 (18)         | 0.11±0.07 (18)   | 34.5±3.5 (20) | 26.4±2.9 (24)                            | 419±41 (24)                                |
| > 130              | 263±58 (30) | 32±5 (30)         | 0.06±0.03 (30)   | 26.5±4.0 (31) | 26.6±4.2 (35)                            | 528±101 (35)                               |

## Supplementary material

### Analysis of turbulence variation and uncertainty

Temporal variation and uncertainty associated with the shear probe measurements were assessed at a time series station, T1, located on Tr2 (57.287 °N, 7.758 °E; 62 m deep) starting 20 July 23:25 and ending 21 July 21:44 (Fig. S1). In total, 107 profiles were made to ~50 m depth in three sequences during the period with typically ~3 minutes between each cast. The temporal variation showed a modest change in temperature between 10-20 m (Fig. S1a) and a relatively small dissipation of turbulent kinetic energy (TKE) at mid-depth during the first 6 hours of the measurements (Fig. S1b). The instrument was equipped with two shear probes and the dissipation of TKE ( $\epsilon$ ) was calculated from each of the probes. The difference between these two estimates, made across the same water volume, are analysed below to assess the uncertainty of the  $\epsilon$ -values.

Samples above 15 m were disregarded in the error-analysis to avoid any influence from the movement of the ship. The relative difference between the calculated dissipation of TKE ( $\epsilon$ ) obtained from each of the two shear probes (i.e.,  $\epsilon_1$  and  $\epsilon_2$ ) was calculated as:  $\Delta\text{Log}_{10}\epsilon = \text{Log}_{10}(\epsilon_1) - \text{Log}_{10}(\epsilon_2)$ . In total, there were 1145 pairs over the 22h period with a relatively small  $\Delta\text{Log}_{10}\epsilon$  average value of -0.063 and a standard and absolute deviation of 0.23 and 0.14, respectively. We applied the absolute deviation, i.e. the more conservative estimate, as being representative of the uncertainty of the  $\epsilon$ -values. The relative probability distribution of  $\Delta\text{Log}_{10}\epsilon$  showed a qualitative accord with a normal distribution characterised by the average value and absolute deviation (Fig. S1b), although the error-distribution showed a tendency to a broader variance for  $\Delta\text{Log}_{10}\epsilon$  larger than ~0.4. This was also clear from the cumulative probability distribution (Fig. S1d) where the error-distribution deviated from a normal distribution (confirmed by a Kolmogorov-Smirnov test). We considered the largest values of  $\Delta\text{Log}_{10}\epsilon$  to indicate sources of errors which could not be directly related to the instrument but potentially associated with the measurement procedure, for example influence from the rope on the free-falling instrument (all casts were made with free and undisturbed line to the free falling instrument during the whole cast). Therefore, we applied the criterion that only measurements where  $\Delta\text{Log}_{10}\epsilon$  was less than 3 times the absolute deviation (i.e. 0.42) were considered to be acceptable and these were included in the analysis. This criterion eliminated only a small number of the  $\epsilon$ -values from the data set.

Temporal variation was also considered from the time series measurements at T1. Variation of  $\epsilon$  is expected to vary due to tides, wind, breaking internal waves etc. Therefore, variations at a single time series station cannot be expected to be representative for the data set as a whole. However, the short-term temporal variation was analysed from samples of  $\epsilon$  binned in 5 m intervals and analysed over a period of 30 minutes (i.e. 11 casts) resulting in average values and absolute standard deviations of  $1.6 \pm 0.6$ ,  $1.4 \pm 0.6$  and  $2.1 \pm 1.0$  in depth intervals between 25-30m, 30-35m and 35-40m, respectively (in units of  $10^{-9} \text{ W kg}^{-1}$ ). Thus, short term variation was relatively small and temporal changes between subsequent casts were considered to have a small influence on the calculated  $\epsilon$ -values. Therefore,  $\epsilon$ -values were, in general, derived from a single cast between the relatively closely spaced stations, where the  $\epsilon$ -value obtained by averaging the calculated value from the two probes was reported. In addition to the time series station, T1, a similar time series station (T2) located at Tr4 is discussed in the text.

## Supplementary figure legends

**Figure S1** Turbulence measurements from time series station, T1, located on Tr2 (57.287 °N, 7.758 °E) starting 20 July 23:25 and ending 21 July 21:44. (a) Temperature (°C) and (c) turbulent kinetic energy dissipation ( $\epsilon$ ,  $\text{W kg}^{-1}$ ) were measured in 107 profiles (small bullets) in three sequences during the 22h period and are shown as a function of pressure and time (Day of the Year). (b) The error-distribution ( $\Delta\text{Log}_{10}\epsilon$  in units of  $\text{Log}_{10}(\text{W kg}^{-1})$ , see text) between calculated  $\epsilon$  from the two shear probes (gray bars) and the normal distribution (green) associated with the average and absolute deviation of the error-distribution. (d) The cumulative probability of the error-distribution (black) compared with the associated normal distribution (green).

**Figure S2** Example of incubation results. Incorporation of carbon (photosynthesis) is shown versus PAR for the surface (5 m, bullets) and the SCM (diamonds) and non-linear best fit solutions (lines) from stations located at a) Tr1, 57.832 °N, b) Tr2, 57.480 °N and c) Tr2, 56.261 °N (cf. Fig. 1a). The following results are obtained from the (surface, SCM) at a):  $P_{\text{max}}^* = (2.5, 3.2) [\mu\text{g C h}^{-1}]$ ,  $\alpha = (0.027, 0.074) [\mu\text{g C} \cdot (\text{h } \mu\text{E m}^{-2} \text{ s}^{-1})^{-1}]$ ,  $\beta = (0.0013, 0.0088) [\mu\text{g C} (\mu\text{E m}^{-2} \text{ s}^{-1} \text{ h})^{-1}]$  and  $E_{\text{max}}^* = (338, 141) [\mu\text{E m}^{-2} \text{ s}^{-1}]$ ; b):  $P_{\text{max}}^* = (4.2, 2.3)$ ,  $\alpha = (0.050, 0.057)$ ,  $\beta = (0.0019, 0.0056)$  and  $E_{\text{max}}^* = (282, 130)$  (units as in a); and c):  $P_{\text{max}}^* = (1.0, 1.2)$ ,  $\alpha = (0.012, 0.019)$ ,  $\beta = (0.0013, 0.0012)$  and  $E_{\text{max}}^* = (284, 219)$  (units as in a). Chlorophyll normalized values (i.e.  $P_{\text{max}}^{\text{B}*}$ ,  $\alpha^{\text{B}}$  and  $\beta^{\text{B}}$ ) are obtained by dividing with the chlorophyll a concentration at the three stations: a) (0.52, 0.95), b) (0.38, 0.82) and c) (0.26, 0.38)  $\text{mg chl a L}^{-1}$ .

**Figure S32** Distributions along the five transects of (a) vertically integrated chlorophyll a ( $\text{mg chl a m}^{-2}$ ), (b) primary production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ), (c) nutricline depth (m), (d) maximum nitrate flux into the euphotic zone ( $\text{mmol N m}^{-2} \text{ d}^{-1}$ ) and (e) f-ratio in euphotic zone. Repeated stations on Tr2 and Tr4, separated in time by about a week, are shown with bullets and open circles.