Vol. 70: 141–155, 2013
doi: 10.3354/ame01649

AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol

Published online August 22

FREE ACCESS

Interaction of productivity and disturbance in a marine ciliate community: a mesocosm study

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ABSTRACT: The intermediate disturbance hypothesis (IDH) predicts that disturbances of moderate frequency or intensity result in maximum diversity, while the dynamic equilibrium hypothesis (DEH) proposes that disturbance and productivity interact in their effects on diversity. These hypotheses were tested with a marine ciliate community in a mesocosm study conducted in a Norwegian fjord. Two nutrient regimes, 6 disturbance frequencies (undisturbed to daily disturbed) and 2 replicates for each treatment were used. To disturb the system, we repeatedly lowered and raised a disk to mix the water column. The experiment lasted 3 wk, with samples (7 including the initial sample) taken for nutrients and physical parameters, chl *a*, ciliates and mesozooplankton. The system reacted more strongly to nutrient addition than to our chosen range of disturbance frequencies. Nutrient addition resulted in higher chl *a* levels and ciliate abundance but reduced ciliate diversity without changing the mean ciliate species richness. The reduction in diversity was due to the very strong, positive response to nutrient addition by the mixotrophic *Mesodinium rubrum*. In contrast, metazoan predators on ciliates (primarily copepods) did not respond to any of the experimental manipulations, at least partially due to the duration of the experiment relative to their generation times. While disturbance had varied and at times marked effects on the mesocosm communities, the expected unimodal response to disturbance frequency was not seen, nor was the expected interaction between disturbance and productivity. While the IDH and DEH have intuitive appeal, they appear to have limited power to predict natural ciliate community patterns.

KEY WORDS: Disturbance · Dynamic equilibrium · Nutrients · Ciliates · *Mesodinium rubrum*

INTRODUCTION

It has long been known that plankton diversity is higher than expected from the low number of niches in the pelagia. Hutchinson (1961) suggested that a gradual change of the environment leads different species to be superior competitors at different times, while the intermediate disturbance hypothesis (IDH) suggests that discrete disturbances would produce a unimodal peak in species diversity at a medium disturbance frequency or intensity (Connell 1978). Although disturbance is often associated with the de-

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struction of biomass, a more general definition, also used for aquatic systems, is the resetting of conditions that would otherwise allow a single species to dominate (Pickett & White 1985, Reynolds 1995, Flöder & Sommer 1999). Events that deepen or destroy stable thermal stratification have been seen as disturbances in this sense, with both observational and experimental studies to support this view (Eckert & Walz 1998, Lindenschmidt & Chorus 1998, Flöder & Sommer 1999). A mesocosm experiment with a freshwater plankton community demonstrated that an intermediate mixing frequency (6 to 10 d) produced the highest phytoplankton diversity, whereas no disturbance effect could be seen on zooplankton (Flöder & Sommer 1999).

Whether and how protists other than phytoplankton respond to disturbance is not clear. The diversity of benthic rhizopods from a frequently resuspended environment did not respond to disturbance in the form of resuspension, nor did the diversity of protists from temporary habitats respond to drying events (McGrady-Steed & Morin 1996, Garstecki & Wickham 2003). Assembly rules and presence of predators can strongly interact with the impact of disturbance on protist diversity, and even when disturbance and diversity are coupled, the mechanism responsible can be different at different spatial scales (Kneitel & Chase 2004, Jiang & Patel 2008, Limberger & Wickham 2012). Moreover, a meta-analysis found no significant diversity–disturbance relationship that supports the IDH as a general trend in ecology (Mackey & Currie 2001). A similar conclusion was reached by Scholes et al. (2005), who examined the combined effect of nutrients and disturbance in a microcosm experiment (including protists) and found no general unimodal trend. Thus, while intuitively appealing, it is not yet apparent how and when the IDH provides a suitable explanation for the structuring of plankton communities in general and of planktonic protist communities in particular.

Productivity is a second factor that has traditionally been thought to interact with diversity to produce a unimodal relationship similar to that for disturbance, i.e. maximum diversity at intermediate productivity (Tilman & Pacala 1993). A variety of factors have been shown to influence this relationship, including the spatial scale (local vs. regional), community assembly rules and stoichiometry (Chase & Leibold 2002, Fukami & Morin 2003, Hillebrand & Lehmpfuhl 2011). In aquatic systems, the evidence for the strength and type of productivity–diversity relationship is mixed. While unimodal relationships have been found for productivity and algal or bacterial diversity, this is not always the case for these or other aquatic groups, and the cause for the relationship is open to interpretation (Leibold 1999, Jeppesen et al. 2000, Kassen et al. 2000).

How ciliate diversity responds to a nutrient gradient is not clear. At a regional scale, a linear relationship between ciliate species richness and productivity has been shown, as predicted by theory (Chase & Leibold 2002, Zingel et al. 2002). However, at a local scale, epibenthic ciliate diversity did not respond to nutrient addition, and it is known that the community assembly sequence has a major impact on the shape of a productivity–diversity relationship (Fukami & Morin 2003, Wickham et al. 2004). Moreover, at least some extremely low productivity systems harbour remarkably high ciliate diversity (Claessens et al. 2010). Thus, how ciliate diversity should respond to changes in productivity is not obvious.

In natural systems, it is to be expected that species are simultaneously exposed to disturbance and nutrient gradients. Huston (1979), with the dynamic equilibrium hypothesis (DEH), suggested that in low-productivity environments, repeated disturbance should drive slow-growing species beneath extinction thresholds, thus lowering diversity. In high-productivity environments, however, growth rates will be high enough that all but the most severe disturbances should enhance diversity by reducing the abundance of the competitive dominant. As a result, whether disturbance reduces or enhances diversity should depend on the productivity of the system. While intuitively appealing, it is not yet clear if and when Huston's hypothesis can be confirmed. A test of the Huston model using protists in microcosms found that while protist species richness was influenced by productivity and disturbance, there was rarely interaction between the 2 factors, and the expected unimodal response to either disturbance or productivity was seldom present (Scholes et al. 2005).

To test the influence and interaction of nutrients and disturbance on a marine plankton community, we conducted a mesocosm experiment with a marine plankton community in a small Norwegian fjord. As nutrient enrichment and disturbance play a major role in coastal marine communities, this system is ideal to test the influence and interaction of these factors on the plankton community. Coastal waters are often nutrient-rich due to anthropogenic effects, upwelling or resuspension of organic material from sediments (Mann & Lazier 2006). Moreover, with the effect of storms magnified by shallow water, the coastal barrier and tidal currents, disturbance is an important factor in structuring coastal marine communities.

The focus of our study was to investigate how ciliate species dynamics were influenced by nutrients and disturbance frequency and if there were diversity patterns as predicted by Huston (1979) and Connell (1978). The experiment was predicated on the following 3 hypotheses:

1) Mixing the water column acts as a disturbance in the sense of the IDH.

2) An intermediate mixing frequency maximizes ciliate diversity.

3) Nutrient addition interacts with disturbance frequency. This interaction results in a maximum ciliate diversity at a higher mixture frequency in nutrient-enriched treatments than in treatments without additional nutrients. Moreover, the maximum mixing frequency should result in higher diversity in the nutrient-enriched treatments than in controls without additional nutrients.

MATERIALS AND METHODS

The experiment was conducted in Sletvik, Norway in the Hopervågn fjord, ~45 km northeast of Trondheim (63° 35′ 38″ N, 9° 32′ 46″ E). The fjord has a maximum length of 0.85 km and a maximum depth of ~35 m. The depth under the raft to which the mesocosms were fixed was ~25 m. Hopervågn fjord is connected to the open ocean by a small tidal inlet, has a total volume of 5.5×10^{-3} km^3, a daily tidal flux of $6.1 \times 10^{-4} \pm 2.2 \times 10^{-4}$ km^3 with minimal freshwater input and a surface area of 2.75×10^{-1} km^2 (Öztürk & Bizsel 2003).

The 24 mesocosms were fixed on a raft in the middle of the fjord where the current was at a minimum. Mesocosms were made out of white polyethylene tubing (Renoplan) with a length of 10.4 m and a diameter of 0.92 m (~7000 l). They were open to the atmosphere and closed to the bottom and were arranged in a 4 × 6 pattern with the treatments randomly assigned. They were filled by lowering the entire mesocosm to ca. 10 m depth and then lifting. To decrease predation pressure, initial zooplankton abundance was reduced to ca. one-third of the initial abundance by repeated hauls from top to bottom of the mesocosms with a 250 µm mesh plankton net.

The experimental design included the presence (+nutrients) or absence (–nutrients) of additional nutrients (phosphorous, nitrogen and silicon, see below), cross classified with 6 different disturbance frequencies (every 1, 2, 4, 8 or 16 d as well as an unmixed control with a nominal mixing frequency of 23 d, the length of the experiment) with 2 replicates per treatment combination (24 mesocosms in total). With expected generation times of phytoplankton and heterotrophic protists on the order of 1 to 2 d, given the water temperature during the experiment (Table 1), we expected the disturbance regime to range from severe to quite moderate. +Nutrients mesocosms received 0.016 µmol P l^{-1} d^{-1}, 0.258 µmol N l^{-1} d^{-1} and 0.258 µmol Si l^{-1} d^{-1}, added on a daily basis. Nitrogen was added 1:1 as ammonium (NH_3) and nitrate (NO_3^-), and P was added as PO_4^{3-}, at the Redfield ratio, modified for diatoms by adding silica (C:Si:N:P: 106:15:16:1; Brzezinski 1985). Nutrients were added with a hose lowered to the bottom of the mesocosm and then slowly raised to ensure an even distribution of nutrients in the water column. Because the experiment was conducted in a fjord with a strong tidal influence, the +nutrients mesocosms had a nutrient regime closest to *in situ* conditions, as the amount of nutrients added compensated for the sedimentation loss and the lack of tidal input.

Table 1. Conditions of the mesocosm experiment, measured 27 July 2009, prior to experimental manipulations

Parameter	Mean (± SD)
Temperature (°C)	12.1 (±0.6)
Salinity	31.6 (±0.6)
C:P	183 (±18)
Particulate phosphorus (µg l^{-1})	5.55 (±0.99)
Chlorophyll *a* (µg l^{-1})	1.85 (±0.97)
Total ciliate abundance (ind. ml^{-1})	11.0 (±6.1)
Mesodinium rubrum (ind. ml^{-1})	8.9 (±5.6)
Ciliate species richness	6.3 (±0.8)
Ciliate diversity (Shannon index, *H'*)	0.73 (±0.23)
Copepods (copepedites and adults; ind. l^{-1})	3.6 (±0.9)

The disturbance was the complete mixing of the mesocosm water column by lowering a Secchi disk with a 70 cm diameter (75% of the mesocosm diameter) to 10 m depth and raising it to the surface, repeating the procedure 4 times per mesocosm. This method has been shown to be effective in mixing mesocosms, with minimal damage to the organisms within (Striebel et al. 2013). The mesocosms were filled on 26 July 2009 with the initial samples being taken on 27 July (prior to nutrient addition and, in the daily mixed treatment, mixing) and the experiment running a further 22 d until 18 August 2009.

Samples were taken with a 2 m long Ramberg tube (2 to 3 l sample per lift) at the same time (starting at 05:00 h) every fourth day prior to mixing and nutrient addition (except the last sample, which was taken 2 d after the previous sampling). The sampling interval

was chosen to be short enough to capture the relevant population dynamics given the expected growth rates at the experimental water temperature, without generating a non-manageable number of samples. For ciliate samples, shallow and deep samples were pooled and fixed with Bouin's solution (5% final conc.). Zooplankton were taken as an integrated sample over the whole water column with a plankton net (250 µm mesh size, 530 l filtered water) and fixed with formalin (5% final conc.).

Ciliates were separated in 7 morphotypes: *Strombidium, Strobilidium, Mesodinium, Laboea, Tontonia,* tintinnids and small oligotrichs and counted in a settling chamber using a Nilon TE 200-U inverted microscope under 200× magnification. These data were used for quantitative analysis. For more exact species determination, quantitative protargol stain (QPS) filters were made for selected samples (Montagnes & Lynn 1987, Skibbe 1994). The Shannon index (*H'*) was used as a diversity measure, utilizing ciliate abundances from Bouins-fixed samples. The main literature used to identify ciliates was Petz (1999), Lynn & Small (2000) and Strüder-Kypke et al. (2002). Zooplankton were counted and identified under a dissecting microscope.

Chlorophyll *a* (chl *a*) was measured *in vivo* based on a chl *a* calibration curve using a fluorometer. The data measured *in vivo* directly after sampling were compared to chl *a* concentrations measured after filtration on a GFF filter (Whatman), storage at –20°C and extraction with acetone (dark and cold for 24 h) on a fluorometer also calibrated with a chl *a* standard (Sigma C6144). Because both measurements provided comparable results, we used the *in vivo* measured chl *a* concentrations as they represent the concentrations measured immediately after sampling. Particulate phosphorus (PP) was measured using the molybdate method (Wetzel & Likens 2000). Chl *a* and PP were measured for shallow and deep layers separately (0–4 and 6–10 m) as it was expected that these 2 parameters were most likely to show depth differences. Temperature, density and salinity profiles were measured every 4 d using a SD204 CTD probe (SAIV A/S). Evenly spaced (0.1 m) profiles were obtained by fitting a smooth spline to the raw downcast profile. Light profiles were measured in 0.5 m steps using a spherical quantum sensor (LI-139SA; Licor). Relative light intensity at a given depth was calculated from simultaneously measured light at the surface and at a given depth. The extinction coefficient (k) was estimated by the formula $I_z = 100 \times e^{(-k \times z)}$, with I_z being the light intensity at depth z.

Data were analysed using repeated measures ANOVA, with sampling date, nutrient addition and disturbance frequency all as fixed factors. Because there were only 2 replicates per treatment combination and therefore low power to discern real differences, differences were declared significant with $p < 0.05$ and a weak trend with $p < 0.1$. Statistical analyses were conducted with R 2.13.2 GUI 1.36 (5691) and SAS v9.2 (SAS Institute 2008, R Development Core Team 2012). To test whether there was a linear or unimodal response of diversity to disturbance, quadratic regression was used, with both disturbance frequency and frequency^2 in the model. To equalize variance across treatments, ciliate abundances and chl *a* concentrations were $\log_{10}$-transformed. In the figures, however, data have been back-transformed to a linear scale.

RESULTS

Physical parameters

The water captured for the experiment was typical of that in the fjord. The difference between the densities measured inside and outside the enclosures was on average 0.6 g l^{-1} at the beginning of the experiment, and the average difference never exceeded 3.6 g l^{-1}. Average initial water temperature within the mesocosms was 12.1°C (Table 1) and, due to the high surface:volume ratio of the mesocosms, was always similar to the temperature of the surrounding fjord water. Temperatures varied mostly from 12 to 14°C throughout the experiment, with a maximum of 16°C (near-surface water, 8 August). The initial C:P ratio was 183 (Table 1), indicative of moderate nutrient limitation. PP was initially 5.5 µg l^{-1} but quickly diverged between treatments (Fig. 1). By the end of the experiment, PP was twice as high in +nutrients mesocosms compared to –nutrients mesocosms (Fig. 1, Table 2). Mixing frequency had less impact than nutrient addition on PP values, but averaged over the entire experiment, there was a significant mixing effect on PP, with the highest values in the daily mixed mesocosms. A significant 3-way interaction indicated that both the difference in PP between nutrient treatments and among mixing frequencies became greater over the experiment (Fig. 1, Table 1). To test whether there was a linear or unimodal relationship between PP and mixing frequency, data for the last 4 sample dates were pooled, and an ANCOVA was conducted, with mixing frequency and frequency^2 as continuous factors, nutrients and

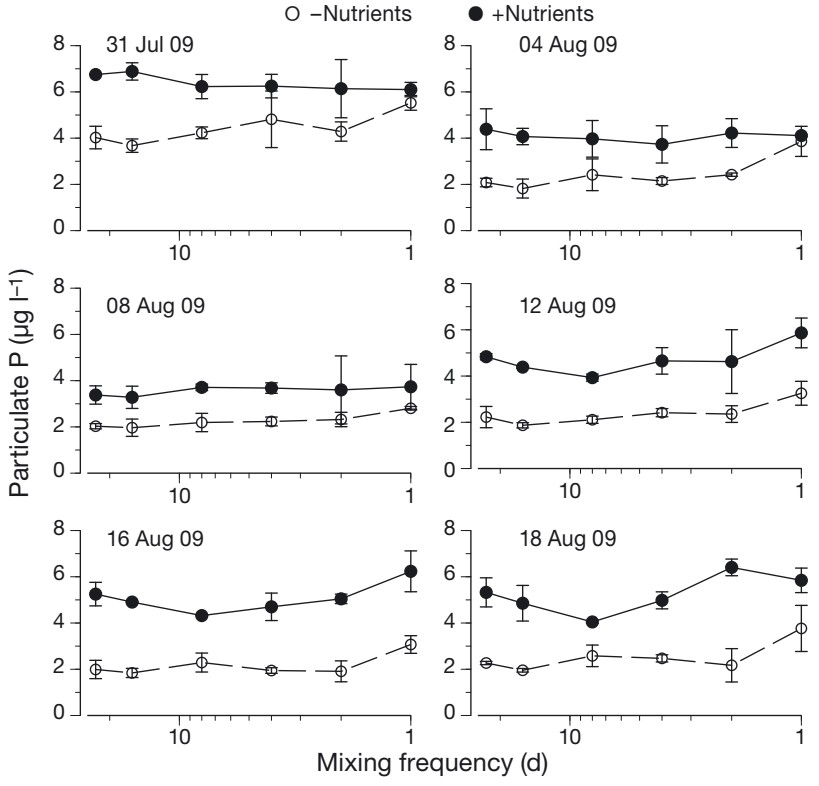

Fig. 1. Particulate phosphorus (µg l^{-1}) plotted against mixing frequency (1, 2, 4, 8, 16 and 23 d intervals) for the 6 sampling dates after the initiation of the experiment. The 23 d interval was the duration of the experiment and is the unmixed control treatment. The mixing frequency axis is reversed in order to have the frequency of disturbance increasing from left to right. Error bars are 1 SD

sampling date as a discrete factor and the interaction between the nutrients and mixing (testing whether the slope of a PP-mixing relationship was dependent on whether nutrients were added). As in the ANOVA, the nutrient term was strongly significant, as was the linear mixing term (both $p < 0.0001$, model $R^2 = 0.81$), with ~27% more PP in the daily mixed mesocosms than in the unmixed controls and the slope of the relationship independent of nutrient addition ($p = 0.57$). The quadratic term was also significant ($p < 0.0001$) but mildly concave, with slightly lower values at intermediate mixing frequencies (Fig. 1). Consistent with increasing PP concentrations with increased mixing, light attenuated more quickly with depth at higher mixing frequencies. There was a weak but still significant negative linear relationship between the attenuation coefficient and mixing, and there was more rapid light attenuation when nutrients were added (mixing effect: $p = 0.014$; nutrient effect: $p = 0.045$; model $R^2 = 0.45$). The light-attenuation coefficients were on average 12% more negative when the mesocosms were mixed daily compared to the non-mixed controls. Thus, over the last 4 sampling dates, increased mixing frequency resulted in a small but significant increase in PP and more rapid light attenuation.

Chl *a*

The initial chl *a* concentration was 1.85 µg l^{-1} in the mesocosms and, as with PP, quickly diverged. Once the experimental manipulations started, chl *a* was ~4-fold higher in in +nutrients compared to –nutrients mesocosms, averaged over the course of the experiment: 0.55 µg l^{-1} and 2.18 µg l^{-1} in +nutrients and –nutrients mesocoms, respectively, a significant difference (Fig. 2, Table 2). However, unlike PP, there was no linear (or unimodal) increase in chl *a* with increased mixing, and in the absence of added nutrients, chl *a* concentrations were essentially constant across mixing frequencies. With added nutrients, the lowest chl *a* concentrations on the last 2 sampling dates were found when mesocosms were mixed every fourth day, but values were 3- to 4-fold higher when mixing occurred every second or eighth day (Fig. 2). In the deep layer, while there was a significant nutrient effect (Table 1), the effect was less than in the shallow layer (~2-fold higher in +nutrients mesocosms, averaged the entire experiment; data not shown). Mixing frequency did not significantly influence deep-layer chl *a* values, partially due to much higher variance between replicates.

Mesozooplankton

Despite pre-filtering the mesocosm water to remove mesozooplankton, low numbers of several groups were present from the beginning of the experiment (Table 1). Most abundant were calanoid copepods, with a mean abundance of 8.4 ind. l^{-1} (adults and copepodites), averaged over all treatments and sampling dates. Copepod nauplii were seen too rarely in either the 250 µm plankton net samples or the settled whole water samples to count accurately or to have a measurable grazing impact. The copepod community was dominated by *Temora longicornis*, but *Centro-*

Table 2. Probability values and model R^2 for repeated-measures ANOVA on the experimental data. 'Date-dependent effects' are the interactions between sampling date and the experimental manipulations. Chlorophyll and ciliate abundance data were $\log_{10}$ transformed to equalize variance across treatments. *H'* is the Shannon diversity measure. Probability values < 0.05 are marked in **bold**

Parameter	Model R^2	Averaged over all dates			Date	Date-dependent effects		
		Mixing interval	Nutrients	Mixing × Nutrients		Mixing interval	Nutrients	Mixing × Nutrients
Particulate P	0.97	**0.025**	**<0.001**	0.375	**<0.001**	0.283	**<0.001**	**0.023**
Shallow-layer chl *a*	0.96	0.744	**<0.001**	0.605	**<0.001**	0.070	**<0.001**	**0.003**
Deep-layer chl *a*	0.87	0.710	**0.002**	0.723	**<0.001**	0.916	**<0.001**	0.500
Total ciliate abundance	0.89	0.116	**<0.001**	0.178	**<0.001**	0.070	**0.001**	0.093
Total ciliates minus *Mesodinium*	0.88	0.502	0.089	0.223	**<0.001**	0.154	**0.026**	0.128
Mesodinium	0.86	0.084	**0.001**	0.237	0.766	0.546	**0.035**	0.095
Strombidium	0.86	0.494	**0.008**	0.202	**<0.001**	0.247	**0.042**	0.302
Strobilidium	0.89	0.802	0.636	0.353	**<0.001**	0.089	0.062	0.108
Small oligotrichs	0.86	0.290	**0.002**	0.086	**<0.001**	0.130	**<0.001**	0.195
Tontonia	0.75	0.562	**0.019**	0.949	**0.010**	0.084	**0.014**	**0.009**
Ciliate species richness	0.61	0.312	**0.011**	0.137	**0.001**	0.642	0.611	0.878
H'	0.92	0.072	**<0.001**	0.090	**<0.001**	**0.011**	**0.011**	**0.006**

pages sp., *Pseudocalanus elongates* and *Acartia longiremis* were also present. Neither the mixing regime nor nutrient addition had any impact on copepod abundance ($p > 0.30$, data not shown). However, the next most abundant zooplankter was moderately enhanced by nutrient addition. The tunicate *Oikopleura* sp. had an abundance of 0.6 ind. l^{-1} and 0.4 ind. l^{-1} in +nutrients and –nutrients mesocosms, respectively, a significant difference ($p = 0.003$, data not shown). There were also low abundances of *Limacina* sp., *Obelia* sp. and *Sarsia* sp. present, but their initial abundances were all <0.05 ind l^{-1}, remaining low throughout the experiment and independent of the experimental manipulations ($p > 0.10$).

Ciliates

Average ciliate abundance was 11 ind. ml^{-1} at the beginning of the experiment, which then decreased in all mesocosms, independent of the mixture frequency or nutrient addition. Without nutrient addition, ciliate abundance remained low, reaching a minimum of 2.3 ind. ml^{-1} on the second non-initial sampling date (4 August) but recovering to ≥4 ind. ml^{-1} by the last 3 sampling dates (Fig. 3). With nutrient addition, total ciliate abundance returned quickly to initial levels, reaching >10 ind. ml^{-1} in the last 4 sampling dates, a significant difference over –nutrients treatments (Nutrient effect: $p < 0.001$; Date × Nutrient interaction: $p = 0.0014$). In contrast, the mixing regime had only a weak effect on ciliate abundance and was dependent on both the sampling date and nutrient addition (Table 2). Mixing had no effect on total ciliate abundance in –nutrients treatments, but higher ciliate abundances were seen when the water column was mixed at 4, 2 or 1 d intervals in +nutrients treatments (Fig. 3). However, there was neither a linear nor monotonic relationship between disturbance frequency and ciliate abundance in the +nutrients treatments, with the highest abundances in the 4 d and 1 d disturbance regimes and intermediate abundances when the water column was mixed every second day.

Ciliate species richness was remarkably consistent across treatments and time. Initial average richness was 6.3 species, and, after the start of the experiment, on average 5.6 morphotypes were found in the mesocosms, with a range of 4 to 7 species (Fig. 4). There were significantly more species found in +nutrients than in –nutrients treatments, but the difference averaged only 0.3 species. There was also a time effect, with a very moderate decline in richness during the middle of the experiment. The decline in

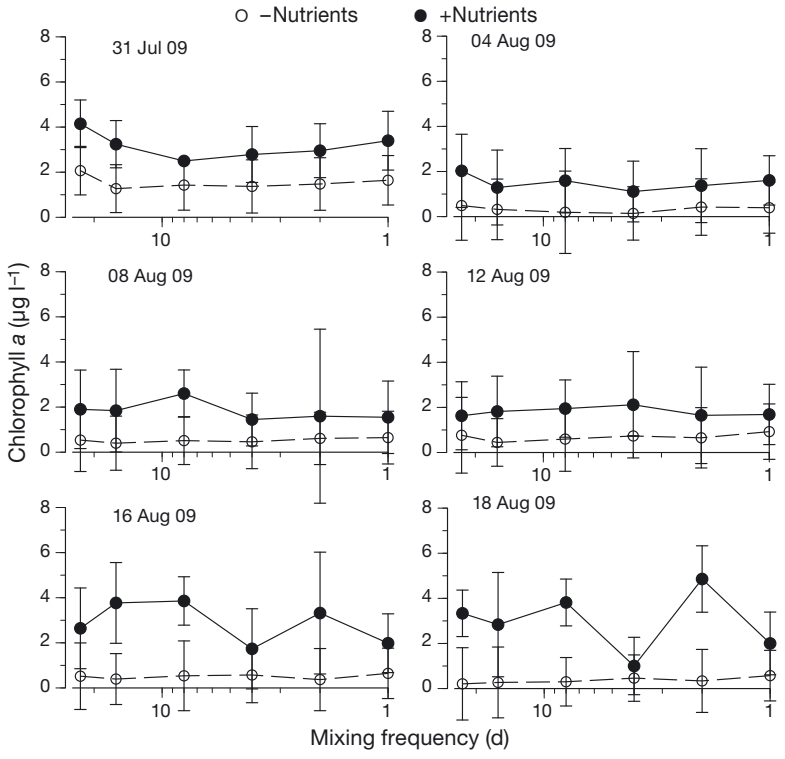

Fig. 2. Chlorophyll *a* (µg l^{-1}) plotted against mixing frequency (23 to 1 d intervals) for the 6 sampling dates after the initiation of the experiment. *x*-axis, symbols and error bars as in Fig. 1. Means and SD are back-transformed from log_{10}-transformed data to make the data equivalent to that used in the repeated-measures ANOVA

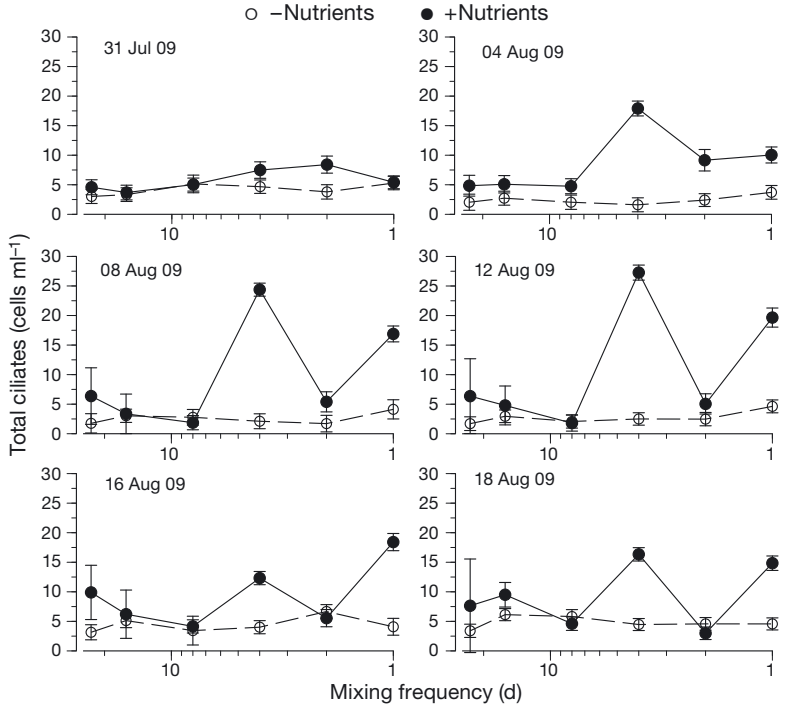

Fig. 3. Total ciliate abundance (cells ml^{-1}) plotted against mixing frequency (23 to 1 d intervals) for the 6 sampling dates after the initiation of the experiment. *x*-axis, symbols and error bars as in Fig. 1. Means and SD are back-transformed from log_{10}-transformed data to make the data equivalent to that used in the repeated-measures ANOVA

richness, however, was much less than the decline in abundance.

In contrast to species richness, species diversity varied strongly, both over time and between treatments (Fig. 5). Averaged over all sampling dates (excluding 27 July, the initial, pre-manipulation sample where diversity was 0.73), *H'* was 1.22 in –nutrients treatments, but only 0.86 in +nutrients treatments, a significant difference (Table 2). Without nutrient addition, there was little difference in diversity between disturbance levels. Pooled over the entire experiment, quadratic regression showed a slight linear decline in diversity with increasing disturbance frequency, but no unimodal response (linear term: $p < 0.0001$; quadratic term: $p = 0.38$). Neither a linear nor a unimodal function could be fit to the +nutrients data. However, in +nutrients treatments, there was considerably more variation among sampling dates and disturbance frequencies. At the middle 2 sampling dates (8 and 12 August), and to a lesser extent the dates directly before and after, the lowest and highest diversities were seen at the 4 d and 8 d mixing intervals, respectively (Fig. 5).

The most abundant ciliate species were *Strombidium* spp. and *Mesodinium rubrum* (formerly *Myrionecta rubra;* Fig. 6). *M. rubrum* was the dominant species throughout the experiment, making up ~75% of the total initial abundance and averaging 52% thereafter, dependent on the sampling date and nutrient addition (Table 2, Fig. 6). Examination of protargol-stained filters showed *Strombidium* spp. to be mostly a mixture of *S. wulffi* and the mixotrophic *S. capitatum*, both between 40 and 60 µm in size. *Strobilidium* spp. were found regularly, but with an average abundance of 0.2 cells ml^{-1} in the initial samples (8% of total abundance) and a maximum of 30% of total abundance subsequently. While a total of 4 tintinnid species could be identified (*Helicostomella subulata, Acanthostomella norvegica, Salpingella acuminatoides* and *Parafavella denticulate*), their collective abundance was also very low, never exceeding 0.15 cells ml^{-1} or 4% of the

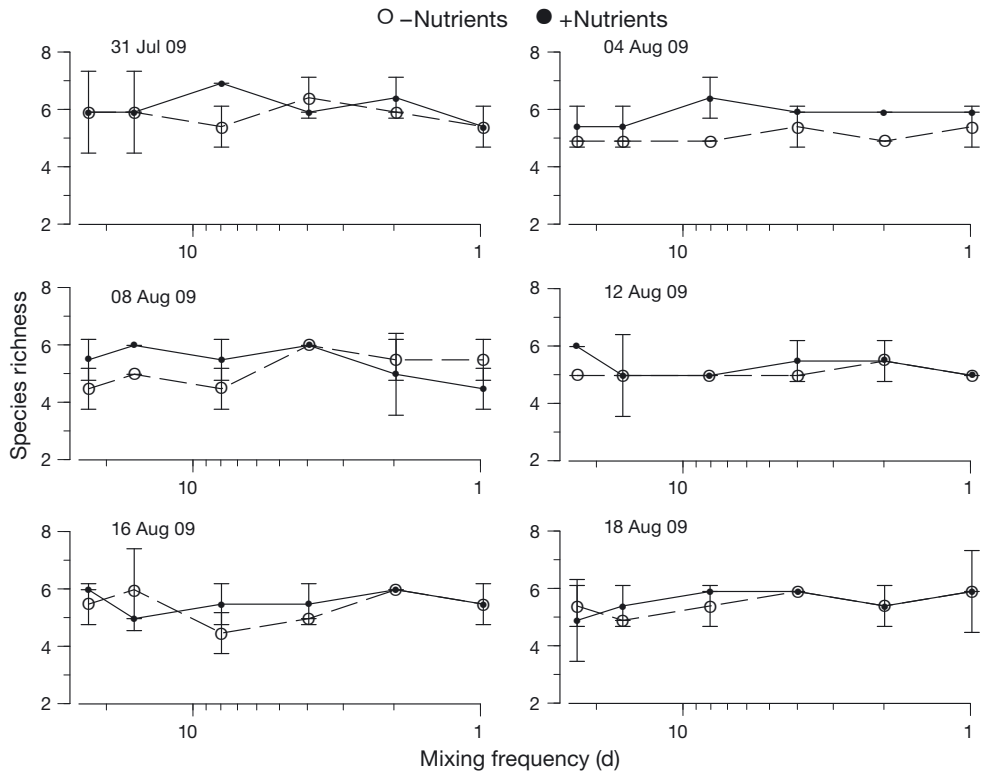

Fig. 4. Ciliate species richness (the number of morphotypes found in settled samples) plotted against mixing frequency (23 to 1 d intervals) for the 6 sampling dates after the initiation of the experiment. *x*-axis, symbols and error bars as in Fig. 1

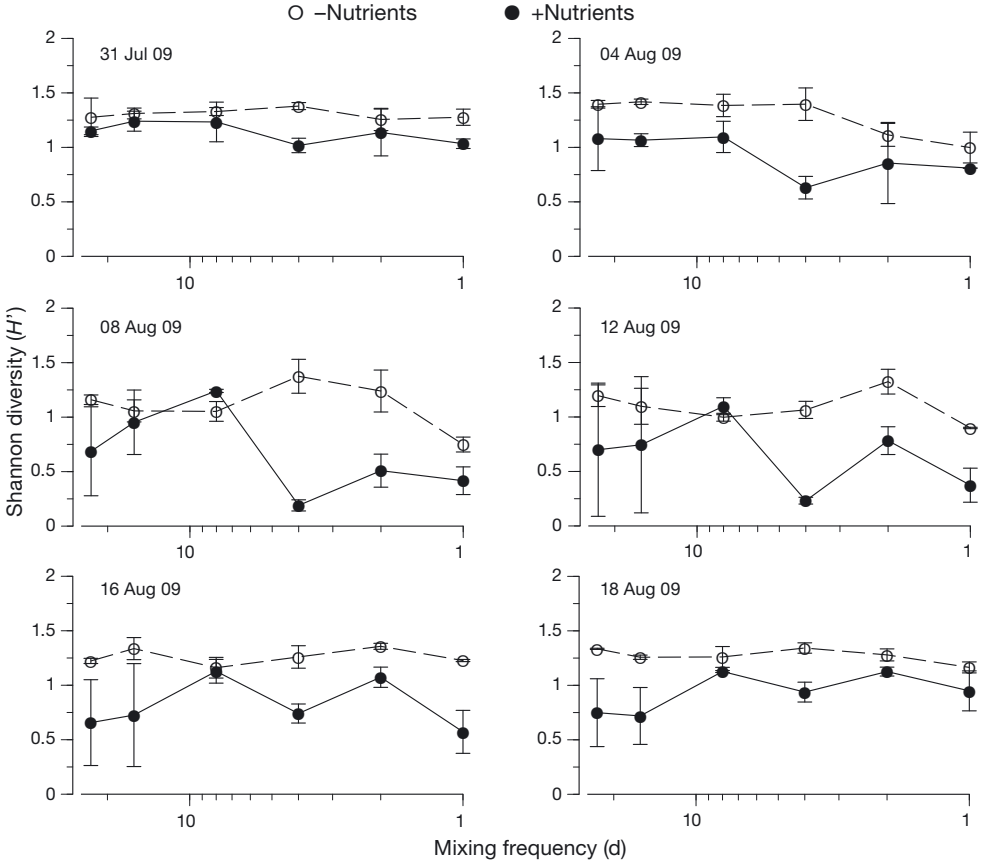

Fig. 5. Ciliate diversity, measured as the Shannon index, plotted against mixing frequency (23 to 1 d intervals) for the 6 sampling dates after the initiation of the experiment. *x*-axis, symbols and error bars as in Fig. 1

total ciliate abundance (Fig. 6). *Laboea strobila* and 2 *Tontonia* species, *T. simplicidens* and *T. gracillima* (all mixotrophic), were also present but also in very low absolute (maximum 0.46 cells ml^{-1}) and relative numbers. Summed over the 19 QPS filters examined, a total of 23 ciliate species were found, indicating that binning took place when counting the settled samples. Most of these species occurred in very low numbers, often occurring only once or twice on all filters. Overlooking rare species resulted in diversity being somewhat overestimated and species richness being underestimated in the settled samples.

Both the increase in total ciliate abundance and the decrease in diversity in +nutrients treatments were mainly driven by an increase in the mixotrophic or autotrophic *Mesodinium rubrum* and, to a lesser extent, *Strombidium* spp. (Fig. 6). Averaged over all treatments and dates, *Mesodinium* abundance was ~3-fold higher in +nutrients compared to –nutrients treatments. In contrast, all other ciliates were collectively only 12% more abundant in +nutrients treatments when averaged over the entire experiment, a non-significant increase (Table 2). There was a significant Date × Nutrient interaction for these ciliates, but the greatest difference in abundance (on 4 August) was 50% higher abundance in +nutrients compared to –nutrients treatments. Without nutrient addition, the general pattern was a decline in the

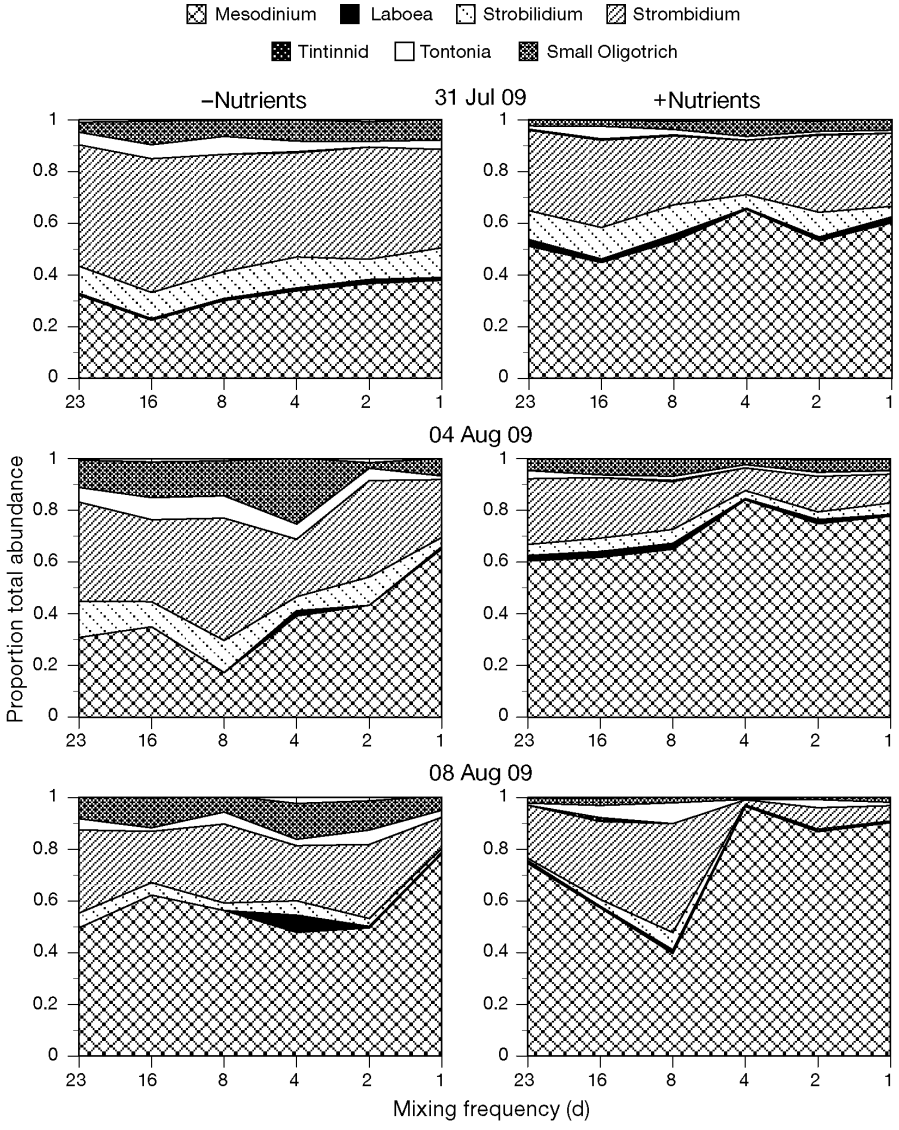

Fig. 6. Proportional ciliate abundance for the main ciliate morphotypes found in the experiment, plotted against mixing frequency (23 to 1 d intervals) for the 6 sampling dates after the initiation of the experiment. (continued on next page)

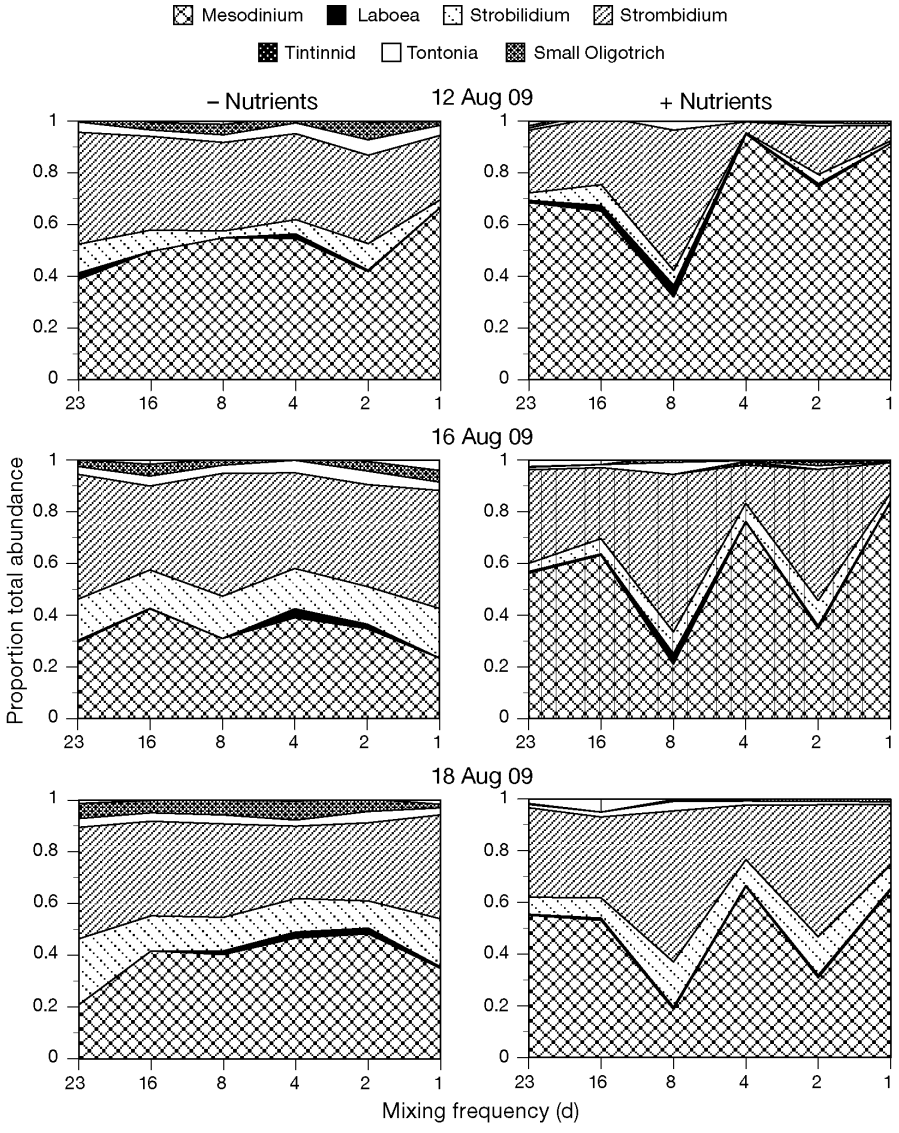

Fig. 6. (continued)

importance of *M. rubrum* from an initial dominance of ~75% of total ciliate abundance to making up between 40% and 60% of the ciliate community, with further declines toward the end of the experiment in the non-mixed, 8 d and 1 d mixing intervals. In marked contrast, when nutrients were added, *Mesodinium* quickly regained or exceeded its initial dominance, particularly in the high-disturbance regimes (4, 2 and 1 d disturbance intervals) during the middle of the experiment (Fig. 6). At its peak (+nutrients, 4 d disturbance interval on 8 and 12 August) *M. rubrum* made up ~95% of the total ciliate abundance. These were also the dates and treatment combinations with the highest total ciliate abundance (Fig. 3).

One reason the non-*Mesodinium* ciliates as a group responded only weakly to nutrient addition was that the individual species responded differently. While *Strombidium* (the most abundant ciliate after *M. rubrum*) responded positively to nutrient addition, the small oligotrichs and the mixotrophic *Tontonia* were less abundant in treatments with added nutrients, while nutrient addition had no significant effect on *Strobilidium* abundance (Table 2, Fig. 6).

While it was expected that *Mesodinium rubrum* and algae would respond similarly to nutrient addition, this was not the case. Pooling all samples, there was no correlation between chl *a* concentrations and *M. rubrum* abundance (Pearson's r =

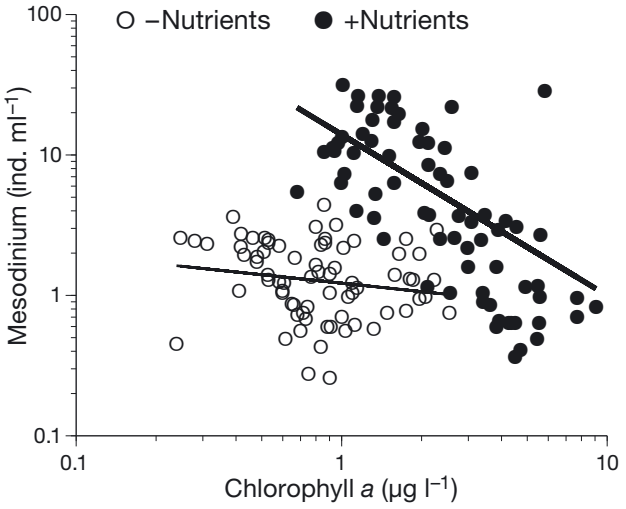

Fig. 7. *Mesodinium rubrum* abundance (cells ml^{-1}) plotted against chl *a* concentration (µg l^{-1}), both on log_{10} scales. Chl *a* was measured separately for the shallow and deep layers but pooled for analysis to make the data compatible with ciliate data. Slopes of the lines are significantly different from one another ($p < 0.0001$), and the 2 lines collectively account for 56% of the variation in *M. rubrum* abundance

−0.01, p = 0.87; both parameters log-transformed). However, splitting the samples by the nutrient treatment showed that 2 separate trends were present. When nutrients were added, there was a strong, negative relationship between chl *a* concentrations and *Mesodinium*, while there was no relationship in −nutrients treatments (Fig. 7; ANCOVA with *Mesodinium* as the dependant variable and chl *a* concentrations as a continuous variable: Nutrient effect, chl *a* effect and Nutrient × chl *a* interaction: $p < 0.0001$, model $R^2 = 0.56$).

DISCUSSION

The 3 hypotheses which the experiment was designed to test were that mixing acts as a disturbance for the ciliate community in Hopervågn fjord, that an intermediate mixing intensity maximized ciliate diversity and that the effect of mixing was dependent on productivity. Previous work has shown that in lake communities, mixing is a disturbance capable of increasing diversity when the disturbance occurred at an intermediate level (Flöder & Sommer 1999). That the ciliates in our experiments did not show any consistent response to the intensity of disturbance raises the question of whether the mixing regime used in the experiment was in fact a disturbance. While Flöder & Sommer (1999) worked in a lake with stable stratification, the present experiment was conducted in a fjord with strong tidal influences and weak density gradients. Due to the tidal water exchange between fjord and the North Sea, salinity and temperature in the fjord changed repeatedly, resulting in an unstable water column in the water surrounding the mesocosms. Svensen et al. (2001) found that background water movement around mesocosms with flexible walls, as were used in our experiment, can mask induced turbulence within the mesocosms. However, unlike Svensen et al. (2001), we could show effects of resuspension: PP increased, and light penetration decreased with mixing frequency, as sedimented material was brought back into the water column by mixing. Moreover, chl *a* concentrations responded strongly to changed mixing frequencies, but only when nutrients had been added. This change, however, was unpredictable, requiring >2 wk to appear and resulting in lowest chl *a* concentrations with mixing every fourth day and higher chl *a* concentrations with both higher and lower mixing frequencies (Fig. 2). Thus, our first hypothesis can be partially confirmed: mixing acted as a disturbance — not in the sense of disturbance destroying biomass, but in moving a system away from equilibrium. However, the overall impact of mixing was quite weak and not in the unimodal fashion predicted by theory.

Our second hypothesis, that ciliate diversity would be maximized at an intermediate mixing intensity, can clearly be rejected. Ciliate species richness did not respond to mixing frequency, and while diversity was dependent on mixing frequency, it was difficult to discern a clear pattern. Without added nutrients, there was a moderate decline in diversity with increasing disturbance, but without the predicted unimodal response. At higher productivity, the response of diversity to disturbance varied greatly over time (Fig. 6). At the middle 2 sampling dates, there was in fact highest diversity in the +nutrients treatments at an intermediate disturbance frequency (8 d); however, this phenomenon could be seen not only in only 2 of the 6 post-initial sampling dates but also at a time when there was considerable variation in diversity at low disturbance and +nutrients. While the relative coarse taxonomic resolution of the settled samples made it impossible to discern fine-scale changes in species composition, it seems unlikely that this masked any clear, unimodal relationship between disturbance and diversity.

The ciliate community itself was fairly typical for coastal or fjord systems. The choreotrichs and oligotrichs that were common in our study have also been

found in more northerly Norwegian fjords and are common to coastal systems (Lynn et al. 1988, Archer et al. 2000). Of the species found, *Laboea strobila*, the 2 *Tontonia* species and *Strombidium capitatum* are obligate mixotrophs, sequestering the chloroplasts of ingested algae (Stoecker et al. 2009). *Mesodinium rubrum* has also previously been found in Norwegian fjords and is common in coastal waters but is capable of forming blooms and was until recently believed to be entirely phototrophic (Crawford 1989, Crawford et al. 1997, Archer et al. 2000).

The third hypothesis that underlays the present study was that there would be an interaction between productivity and disturbance. Ciliate diversity, as measured by the Shannon index, did have a significant interaction between mixing frequency and nutrient addition, albeit on a time-dependent basis (Table 2). However, it would be difficult to say that this was the interaction expected by theory. The DEH predicts that increasing productivity will reduce diversity when disturbance is low but will increase diversity at high disturbance (Huston 1979). On 8, 12 and 16 August, when the diversity differences between the +nutrients and −nutrients treatments were greatest, increased productivity reduced diversity at high disturbance frequencies, directly counter to Huston's hypothesis (Fig. 5). However, while the reduction was less than at high disturbance frequencies, increasing productivity did reduce diversity in the two lowest disturbance frequencies, as predicted by the DEH. This was true when averaged over the entire experiment or averaged over the middle 3 dates ($p < 0.0001$). Why an 8 d disturbance frequency produced the least difference in ciliate diversity between +nutrients and −nutrients treatments is unclear, as the trend is not seen in the ciliate abundance or chl *a* data (Figs. 2 & 3). Having 6 disturbance levels resulted in only 2 replicates per treatment combination, leaving only limited statistical power to detect real trends. However, the patterns and the relatively small standard deviations shown in the figures suggest that more statistical power would not reveal a pattern masked by high variance. Our data largely fail to confirm the DEH.

Despite the intuitive appeal of the IDH and DEH, ours is not the first study to have difficulty in supporting them. A meta-analysis found that <20% of published tests, using a wide range of organisms, supported the IDH (Mackey & Currie 2001). An underlying assumption of the IDH is that there is a trade-off between competitive ability and either colonizing ability or disturbance resistance, with the better competitors dominating when disturbance is weak or rare, and better colonizers or species resistant to disturbance dominating when disturbance is severe (Connell 1978). Some ciliate communities show this trend, although counter examples are also abundant (Haddad et al. 2008, Violle et al. 2010, Limberger & Wickham 2011). Assembly rules (how communities are put together) can also strongly influence whether the expected unimodal response of diversity to disturbance or productivity is seen (Fukami 2001, Jiang & Patel 2008), but this should not have played a role in our experiment. The ciliates found in our samples all occur together by nature of the experiment, and the volume of the enclosures (7000 l) was large enough that initial differences in ciliate community composition were minor. No differences could be found in the initial ciliate abundance or diversity, nor were there differences in the initial chl *a* or PP concentrations ($p > 0.25$).

Disturbance in natural systems often serves to make more resources available (e.g. through destruction of old biomass), thus potentially confounding the effects on diversity of manipulating productivity (Scholes et al. 2005). If there is a positive relationship between disturbance and release of nutrients, then high-disturbance systems would also be high-productivity systems. In our experiment, however, this was not the case. While PP increased with more frequent mixing, there was no effect of mixing on shallow-layer chl *a* (the main resource for ciliates) averaged over the experiment and only a marginal effect dependent on time, with the differences in chl *a* concentrations between disturbance levels increasing somewhat over the course of the experiment (Table 2, Fig. 2). There was a significant disturbance–nutrient–time interaction ($p = 0.003$), but this manifested itself in the form of relatively low chl *a* concentrations on the last 2 sampling dates in +nutrients, 4 d disturbance interval treatments (Fig. 2). Had the disturbance effect been confounded by the nutrient effect, then higher disturbance frequencies should have produced higher chl *a* concentrations, independent of the addition of nutrients, and this was clearly not the case.

The lack of the expected interaction between productivity and disturbance has also been found for a laboratory community of bacterivorous protists, which largely failed to consistently show either unimodal responses to disturbance and productivity or the interaction predicted by the dynamic equilibrium model (Scholes et al. 2005). As in our experiment, the time component was critical, with the form of both the diversity–disturbance and diversity–productivity

relationships changing over time. The inability to confirm the DEH in both laboratory and field settings would suggest that the lack of confirmation was not due to the community composition or the experimental setting used in the experiments.

One possible reason for the divergence between theory and the experimental results is that an implicit assumption in most diversity theory is that effects operate on distinct trophic levels, whereas the ciliates found in the experiment encompassed a wide trophic range. There were heterotrophs (e.g. *Strombidium wulfi*), mixotrophs known to both feed and retain chloroplasts (e.g. *Laboea strobila*) and a near-autotroph with a reduced cytostome, questionable ability to ingest anything beyond algae used to sequester chloroplasts and capable of forming large blooms (*Mesodinium rubrum*; Crawford 1989, Crawford et al. 1997, Gustafson et al. 2000). However, if *M. rubrum* is excluded in the diversity measure, the Mixing × Nutrient interaction becomes weaker, both averaged over time and on a time-dependent basis ($p = 0.084$ and $p = 0.82$, respectively). Therefore, the inclusion of *M. rubrum* in the diversity measures did not mask the interaction between disturbance and productivity expected by theory. Moreover, most ciliate communities contain a mixture of mixotrophs and heterotrophs, with *M. rubrum* a common member of marine ciliate communities.

Although the water column was filtered to remove mesozooplankton at the beginning of the experiment, there were low (<9 ind. l^{-1}) numbers of calanoid copepods present throughout the present study. While calanoids are selective predators, it is unlikely that the dominance of the ciliate community by *Mesodinium* was facilitated by selection against *Mesodinium* relative to other ciliate prey. Several studies suggest that *Mesodinium* is grazed by calanoids at rates at or above that for other prey, and while *Mesodinium* has a jumping response, this is ineffective against ambush predators (Jakobsen 2001, Rollwagen Bollens & Penry 2003, Fileman et al. 2007). Copepod abundance between treatments with and without nutrients also did not differ, thus excluding differences in top-down control as an indirect cause of higher *Mesodinium* abundance in +nutrients treatments.

Despite *Mesodinium rubrum* being a common bloom-forming species, there is considerable uncertainty as to both its taxonomic status and autecology. There are at least 3 similar mixotrophic *Mesodinium* species as well as genetic diversity within *M. rubrum*, with not all genetic variants generating blooms (Herfort et al. 2011, Garcia-Cuetos et al. 2012). Furthermore, it is uncertain whether *Mesodinium* only uses the cryptophyte *Teleaulax* sp. as a symbiont or whether other cryptophytes are also utilized (Yih et al. 2004, Johnson et al. 2007, Garcia-Cuetos et al. 2012). While *M. rubrum* has a reduced cytostome and no digestive vacuoles, it is capable of rapidly reducing *Teleaulax* abundance in culture and, when starved, will lose the pink colour acquired from the symbiont (Gustafson et al. 2000).

Our study may add to the confusion surrounding the ecology of *Mesodinium rubrum*. *M. rubrum* is described as being found in well-defined layers, needing calm conditions for blooms to form (Cloern et al. 1994, Crawford & Lindholm 1997, Montagnes et al. 1999, Sjöqvist & Lindholm 2011). Despite this, *Mesodinium* in our experiment was unaffected by mixing, even at daily intervals (Table 2, Fig. 6). *Mesodinium* clearly benefitted from nutrient addition, dominating the ciliate community in +nutrients treatments and increasing relative to −nutrients treatments only slightly less than chl *a* in general (+nutrients vs. −nutrients, averaged over all dates: chl *a*, 4-fold higher; *Mesodinium*, 3.1-fold higher). This would suggest that *Mesodinium* blooms should be more prevalent with coastal eutrophication, but previous reports suggest that the relationship between *Mesodinium* abundance and total chlorophyll is weak (Dolan & Marrase 1995, Suzuki & Taniguchi 1998). In our study, there was either no correlation (−nutrients) or a negative correlation (+nutrients). The negative correlation is not due to *Mesodinium* exerting top-down control on algae, as *Mesodinium*'s maximum individual ingestion rate is <10 cells d^{-1}, saturating at only 44 cells ml^{-1} (Yih et al. 2004). The maximum *Mesodinium* abundance in our experiment was ~30 cells ml^{-1}, giving a community grazing rate too low to exert measurable grazing pressure on algae, particularly in the +nutrients treatment where the negative correlation between *Mesodinium* and chl *a* was found. The reasons for the negative relationship between *Mesodinium* and chl *a* in the +nutrients treatment and the lack of a relationship in the −nutrients treatment and in field studies remains unclear.

How disturbance structures ciliate communities and how changing productivity interacts with disturbance remain open questions. While previous work with artificial communities have had some success in outlining processes that can drive these interactions, the results of our experiment show that in a natural community dominated by a mixotroph, the IDH and DEH appear to have only limited relevance.

Acknowledgements. We thank A. Neyts, Ø. Leiknes and J. Evertsen for support at the field station and A. Wild and A. Weigert for chemical analysis. We also thank H. Stibor, S. Behl, U. Berninger, F. Haupt, C. Mangold, M. Steinböck and S. Wollrab for help with the experiment. This work has been supported by the European Community's Sixth Framework Program through a grant to the budget of the Integrated Infrastructure Initiative HYDRALAB III within the Transnational Access Activities, Contract no. 022441.

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Editorial responsibility: Robert Sanders, Philadelphia, Pennsylvania, USA

Submitted: October 18, 2012; Accepted: June 13, 2013
Proofs received from author(s): August 9, 2013