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Low frequency offshore wind farm noise affects natural planktonic communities during an in situ microcosm experiment in Norwegian coastal waters

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Abstract

The effects of anthropogenic underwater noise, such as operational noise from offshore wind farms (OWFs), on plankton are poorly understood. A significant challenge in assessing the impact of noise on natural communities is the lack of holistic and ecologically relevant experimental setups mimicking soundscapes and communities under close-to-natural conditions. To address this, we conducted a 22-hour bottle incubation experiment using real OWF recordings broadcast underwater, creating three distinct sound exposure levels: High Noise with an average sound pressure level of 106 dB re 1µPa, Medium Noise at 94 dB re 1µPa and the Control, only experiencing the ambient sound at 80 dB re 1µPa, (over 50–2400 Hz band). At the community level, changes in phytoplankton growth, zooplankton grazing, and oxygen concentrations were assessed across treatments. After a 22-hour exposure, phytoplankton growth rates were significantly higher under noise exposure. This was concurrent with a more positive net oxygen balance suggesting higher primary production when the community was exposed to OWF noise. However, grazing rates did not differ significantly among experimental conditions. This study implemented a new experimental methodology and demonstrated that short-term OWF noise exposure significantly impacts phytoplankton growth rate and oxygen balance, but not zooplankton in a coastal lagoon.

Introduction

The increasing prevalence of underwater anthropogenic noise represents a growing threat to marine life[1]. While there is an increasing body of knowledge on the effects of noise pollution on marine mammals and fish[2,3], significant knowledge gaps remain regarding its impacts on lower trophic levels[4]. This is particularly true for invertebrates[5–7] and, even more specifically, for plankton. Plankton, which form the base of marine food webs, are drifters that cannot avoid the soundscape of their environment. Although they lack conventional hearing organs, it is likely that they are affected by underwater sound, either through sound pressure or particle motion and vibration[8–10]. Many planktonic organisms possess sensitive mechanoreceptors, such as setae and cilia, which they use

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to detect vibrations[11] originating from soundwaves[7]. For instance, copepods and bivalve larvae use them to detect prey[12–14], while meroplanktonic larvae in general use them as settlement cues[15,16], thus suggesting that plankton can be affected by anthropogenic noise. Note that in this manuscript, we refer to sounds that originate from human activities in the ocean as noise.

While research on the effects of noise on plankton is scarce, a few studies have assessed potential impacts. For example, low-frequency noise from seismic airgun surveys did not affect lobster larvae development[17] but caused malformations in scallop larvae[18]. Additionally, low-frequency sound has been shown to slow down the development rate of the copepod *Acartia tonsa*[19], while ship noise decreased its feeding rate[20]. Even lower trophic levels (i.e. protists) are reported to be affected by sound. As an example, the unicellular green alga *Dunaliella salina* was stimulated when exposed to sound waves at 100, 200, and 500 Hz played in the air adjacent to the algal tanks, showing increases in growth, biomass, and productivity[21]. Similarly, growth rates of the freshwater microalga *Haematococcus pluvialis* increased with playback of sounds at 240 and 280 Hz[22]. These few studies demonstrate that plankton can respond to human-made noise, particularly at low frequencies, with potential consequences on planktonic communities.

Human activities that produce low-frequency noise include seismic airguns, marine traffic, construction activities, and operating offshore wind farms (OWF). When wind turbines are in operation, they emit relatively constant low-frequency noise below 1000 Hz, with a peak at 50 Hz[23,24]. However, there is a significant gap in our understanding of how OWFs impact plankton and the broader marine food web. This is partly due to the technical complexity and constraints of investigating the impact of noise on plankton using laboratory tanks[25]. More specifically, low-frequency sounds are quickly attenuated in an environment smaller than their wavelength, making it difficult to study the impact in small tanks[26,27]. Additionally, reflections from tank walls distort the spectrum[28,29]. This makes it difficult to compare results across studies and poses a major challenge for assessing the effects of anthropogenic noise on marine life[25]. In contrast, in situ experiments offer a more reliable, close-to-natural approach to assess impacts of noise on aquatic biota. While this approach has its own challenges, it provides a promising alternative to simulate noise pollution and assess its impact on marine ecosystems under controlled, ambient conditions.

In this study, we introduce a novel experimental setup designed to simulate OWF-like low-frequency noise exposure in shallow waters. While not conducted within an operational wind farm, this in situ approach aims to provide a bridge between laboratory tanks and field monitoring. It allows for a controlled acoustic exposure of a natural community while maintaining relatively natural environmental conditions. With this experimental setup, our objective was to test the hypotheses that: (1) low-frequency noise directly alters phytoplankton growth rates through physiological stimulation, and (2) it can negatively affect micro- and mesozooplankton grazing by disrupting the mechanoreceptors involved in the feeding activity. By assessing these responses simultaneously, we aim to determine if low-frequency noise can affect the plankton food web functioning.

Results

Sound exposure treatment

From the measurements conducted in the lagoon of Hopavågen, we determined a **High Noise** treatment location at 15 m from the speaker (63°35.548' N; 9°32.446' E, Fig. 1), with a root-mean-square sound pressure level (SPL_{RMS}) of 106 dB re 1 µPa. A **Medium Noise** treatment, receiving 94 dB re 1 µPa, was situated 35 m from the speaker (63°35.539' N; 9°32.464' E). Finally, a **Control** location was placed 420 m from the speaker (63°35.447' N; 9°32.884' E), where the broadcast signal was undetectable, ensuring that this site experienced only the natural ambient SPL_{RMS} of 80 dB re 1 µPa. The power spectral density (PSD) analysis revealed elevated sound levels at the two treatment sites over the 100–500 Hz frequency range compared to the Control site (Fig. 2).

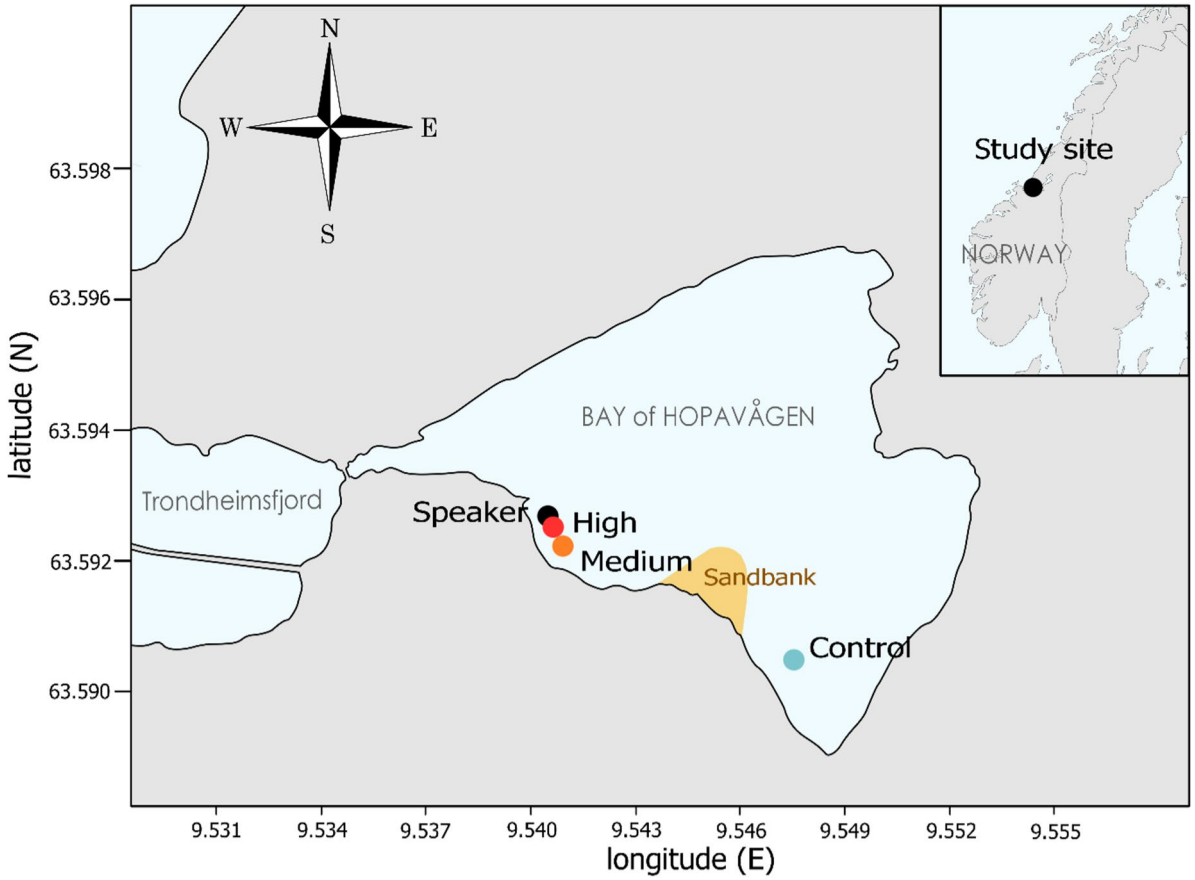

Fig. 1 Location of the UW30-100 underwater speaker and the sites of the Control (blue), Medium (orange) and High Noise treatment (red) in Hopavågen lagoon.

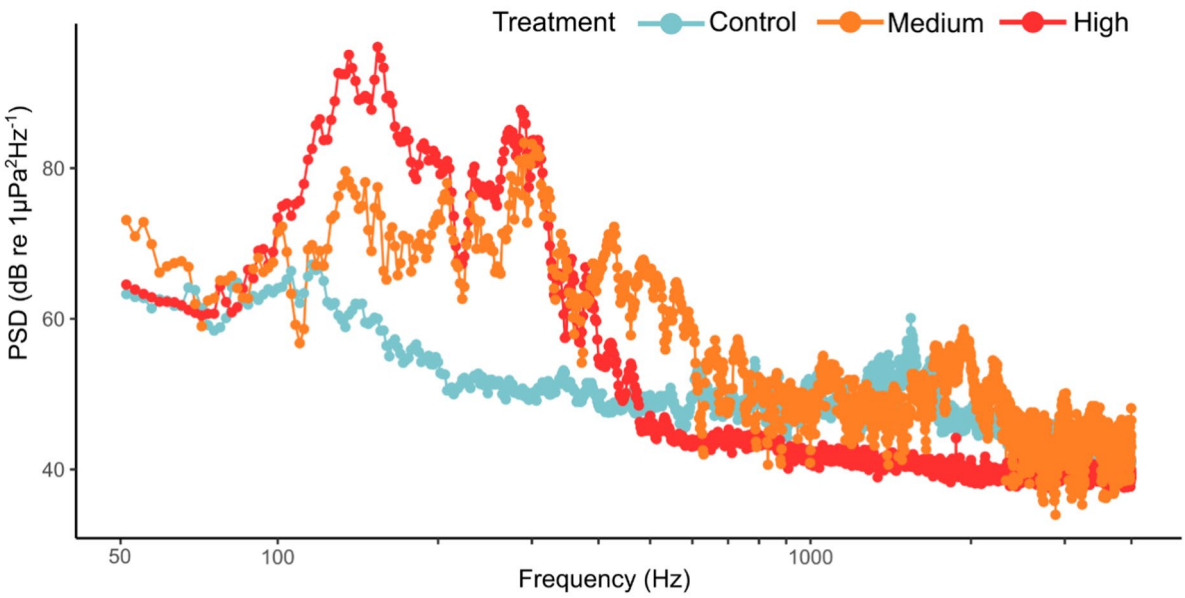

Fig. 2 Power spectral densities (PSD; dB re 1 μPa^2 Hz^{-1}) of sound recordings collected at the High (red), Medium Noise (orange) locations and Control (blue) location in Hopavågen lagoon.

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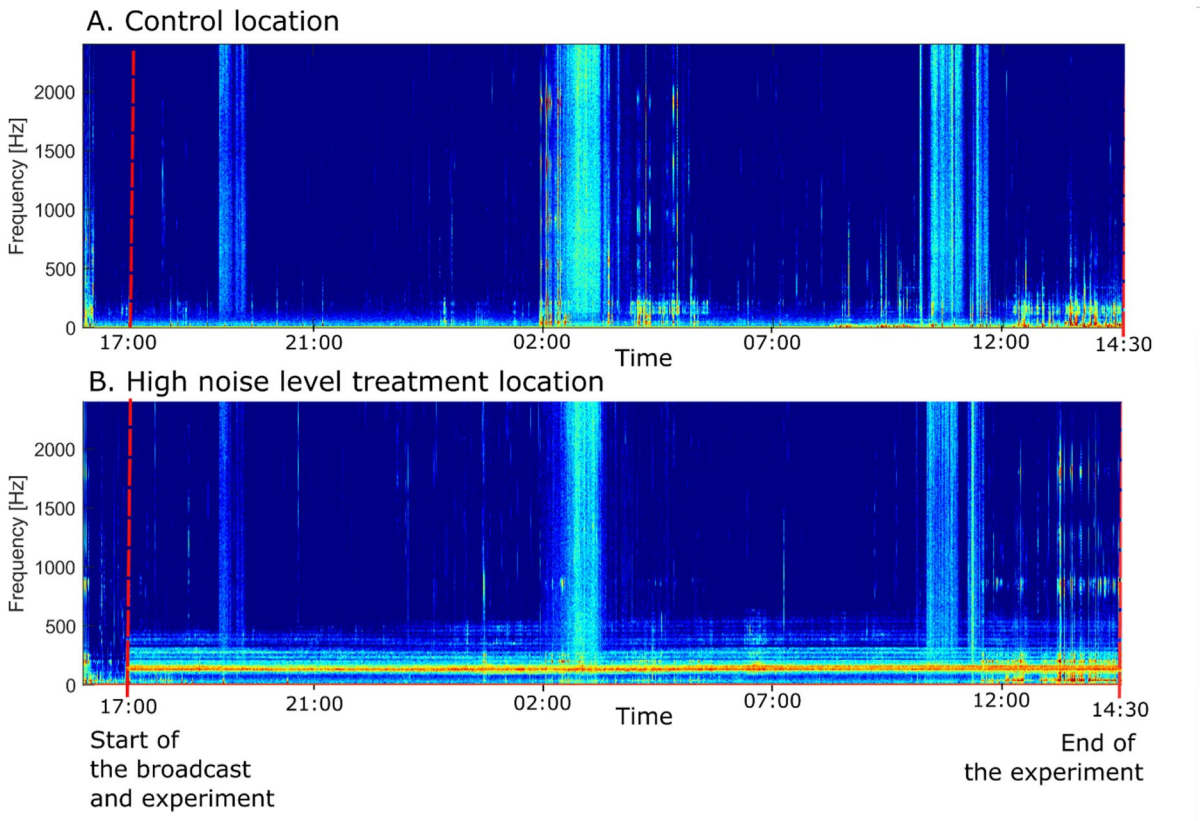

Fig. 3 Long-term spectral average showing the soundscape at the Control (**A**) and High Noise (**B**) treatment location in the Hopavågen lagoon.

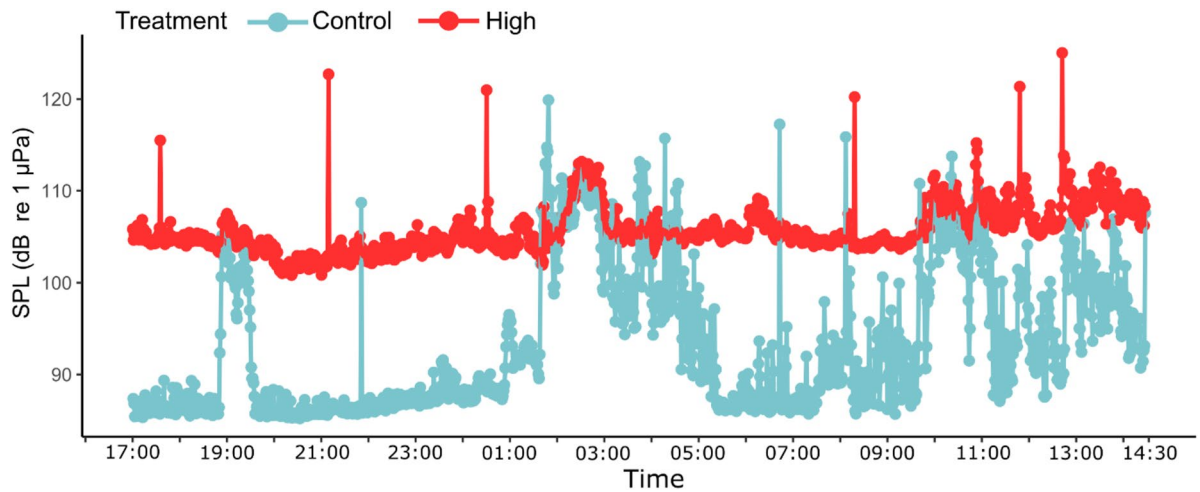

Fig. 4 One-minute SPL_{RMS} over 50–2400 Hz at the Control (blue) and High Noise (red) treatments during the experiment.

Investigation of the long-term spectral average and minute interval SPL_{RMS} calculations revealed that at the Control location, the SPL_{RMS} was below 83 dB re 1 µPa during calm weather. However, during the experiment, windy conditions coupled with wave action occurred in the afternoon of August 13, during the night, and on the afternoon of August 14, temporarily increasing ambient sound levels at both locations (Figs. 3 and 4). In addition, higher sound levels were detected below 300 Hz at the Control location following the two main rainfall events

resulting from the clinking of the metal ring used to attach the concrete block to the buoy line (Figs. 3 and 4). Biological sounds were also recorded toward the end of the experiment at the Control location. Similar signals were also recorded at the High Noise location but were largely masked by the treatment. Despite the bad weather conditions and biological sound during the experiment, the SPL in the noise treatments remained significantly above the elevated ambient sound levels (see Fig. 4).

Environmental conditions

The temperature and salinity measured in the lagoon were quite stable and homogeneous across all locations both before and after the incubation period, ranging from 14.97 to 17.50 °C and from 28.90 to 31.61, respectively within the water column (Supplementary Fig. 1, Supplementary Table 1). Although light was not measured concurrently, continuous sensor data collected in summer 2024 showed no significant difference in light availability at 1 m depth between the Control and the Noise treatment locations over a three-week period (Courboulès J. unpublished data).

Initial phytoplankton pigment concentrations and zooplankton community composition

The main pigments identified were chlorophyll-*a* (Chl-*a*), chlorophyll-*b* (Chl-*b*, marker pigment for green algae[30]), Fucoxanthin (marker pigment for diatoms[30]), and Zeaxanthin (marker pigment for cyanobacteria[30]).

Chl-*a* concentrations were on average 1.10 µg L^{-1} in the <200 µm fraction and 0.82 µg L^{-1} in the unfiltered fraction (Table 1). Fucoxanthin concentrations ranged between 0.25 and 0.28 µg L^{-1} in the two fractions, respectively. Chl-*b* and Zeaxanthin concentrations were low, ranging between 0.04 and 0.08 µg L^{-1} in the different fractions.

Protozoans were present in both the <200 µm and the unfiltered fractions. The protozoan community was clearly dominated by small naked mixo-/heterotroph dinoflagellates (14200 cells L^{-1}, Supplementary Fig. 2) which constituted 51% of protozoan abundance. Other mixo-/heterotroph dinoflagellate taxa were unidentified dinoflagellates (1890 cells L^{-1}) and *Gyrodinium* spp. (1440 cells L^{-1}), comprising 7 and 5% of the total protozoans. Several ciliate taxa were also abundant, including *Strombidium* spp. (2640 cells L^{-1}), *Strombidinopsis* spp. (1930 cells L^{-1}), *Mesodinium* spp. (2910 cells L^{-1}), each contributing 5–10% to the total protozoan abundance.

Metazoans were predominantly found in the unfiltered fraction and much less in the <200 µm fraction. The metazoan community was dominated by copepod nauplii (28.8 ind L^{-1}) and *Oithona* spp. copepodites, which accounted for 38% and 23% of the total metazoan abundance, respectively. A few small metazoans, consisting of copepod nauplii, Appendicularia, Bivalvia and Polychaeta larvae, were occasionally found in the <200 µm fraction and highlighted by a star (*) in Supplementary Fig. 2.

Table 1 Initial pigment concentrations from the unfiltered and <200 µm fractions water used to fill the incubation bottles.

Pigment	Initial concentration [µg L^{-1}] (±standard deviation)	Fraction
Chl-*a*	1.10 (±0.10)	<200 µm
	0.82 (±0.13)	Unfiltered
Fucoxanthin	0.28 (±0.01)	<200 µm
	0.25 (±0.02)	Unfiltered
Chl-*b*	0.08 (±0.01)	<200 µm
	0.06 (±0.02)	Unfiltered
Zeaxanthin	0.04 (±0.01)	<200 µm
	0.04 (±0.02)	Unfiltered

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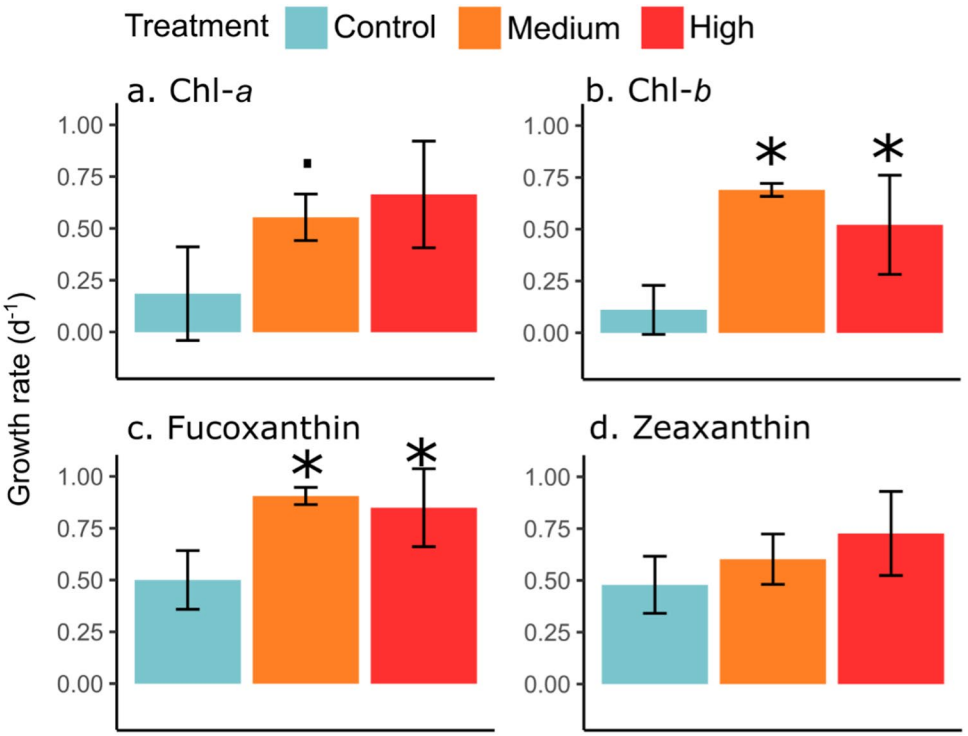

Fig. 5 Phytoplankton growth rates (d^{-1}) estimated from pigment concentration changes with the two-point dilution method in the Control (blue), Medium (orange) and High Noise (red) treatments. Statistically significant differences compared to the Control are highlighted by a star (*) for a p-value < 0.05 and by a dot (.) for a p-value < 0.1.

Table 2 Summary table of relative changes (in %) and p-values (in parenthesis) for growth, grazing and net oxygen change rates across the different treatments. Significant differences among treatments (p-value < 0.05) are highlighted in bold.

Variables	Pigment	C-H	C-M	H-M	Statistics
Growth rate	Chl-a	257% (0.07)	198% (0.16)	-17% (0.80)	F = 4.3539
	Chl-b	**369% (0.04)**	**521% (0.01)**	32% (0.43)	F = 11.031
	Fucoxanthin	**70% (0.05)**	**81% (0.03)**	7% (0.87)	F = 7.5897
	Zeaxanthin	52% (0.21)	26% (0.63)	-17% (0.62)	F = 1.8456
Total community grazing rate	Chl-a	270% (0.44)	-	-	F = 1.7361
	Chl-b	-	-	66% (0.83)	F = 1.1256
	Fucoxanthin	-	-	-23% (0.92)	F = 1.4885
	Zeaxanthin	85% (0.34)	25% (0.89)	-32% (0.56)	F = 1.2419
Microzooplankton grazing rate	Chl-a	152% (0.55)	106% (0.74)	-18% (0.94)	F = 0.6243
	Chl-b	-	-	-	F = 0.6385
	Fucoxanthin	1920% (0.20)	2279% (0.13)	18% (0.93)	F = 3.1517
	Zeaxanthin	69% (0.30)	18% (0.40)	-30% (0.30)	H = 5.0667
Mesozooplankton grazing rate	Chl-a	-	-	-	-
	Chl-b	-	-	61% (0.88)	F = 0.943
	Fucoxanthin	-	-	-	-
	Zeaxanthin	211% (0.96)	81% (0.97)	-42% (0.88)	F = 0.1201
	Fraction				
Daily oxygen net change	Unfiltered	**41% (0.002)**	**44% (0.001)**	5% (0.90)	F = 27.289
	<200 µm	27% (0.26)	25% (0.33)	4% (0.98)	F = 1.8564

Dashes (-) indicate when the percentage of difference could not be estimated, mostly because of rates equal to 0 d^{-1}.

Phytoplankton growth rates

Phytoplankton growth rates were consistently higher in the High and Medium Noise treatments compared to the Control. In the Control, growth rates were generally low, particularly for the chlorophylls (0.18 d^{-1} for Chl-*a*, 0.11 d^{-1} for Chl-*b*) and slightly higher for Fucoxanthin and Zeaxanthin (0.50 d^{-1} and 0.48 d^{-1} respectively) (Fig. 5; Table 2). Chl-*b* growth rates were 369% higher in the High Noise treatment ($p = 0.04$) and 521% higher

in the Medium Noise treatment ($p=0.01$), compared to the Control. Fucoxanthin growth rates were 70% higher in the High Noise ($p=0.05$) and 81% higher in the Medium Noise treatments ($p=0.03$). Chl-*a* and Zeaxanthin growth rates did not show a significant difference between treatments. Nonetheless, Chl-*a* growth rates were 257% and 198% higher, and Zeaxanthin rates were 52% and 26% higher in the High and Medium Noise treatments, respectively, compared to the Control.

Growth rates estimated from the nutrient-amended dilution bottles did not significantly differ from the non-amended bottles (Supplementary Fig. 3), indicating that the phytoplankton community was not nutrient-limited at the time of the experiment.

Zooplankton grazing rates

The estimated grazing rates showed no significant differences among treatments, but grazing rates tended to be slightly higher in the High and Medium Noise treatment compared to the Control (Table 2).

In the Control, total community grazing rates were 0.06 d^{-1} for Chl-*a* and 0.39 d^{-1} for Zeaxanthin, but were 0.0 d^{-1} for the other pigments (Fig. 6). The rates based on Chl-a were 270% higher in the High Noise treatment than Control. Similarly, total community grazing rates for Zeaxanthin were 85% and 25% higher in the High and

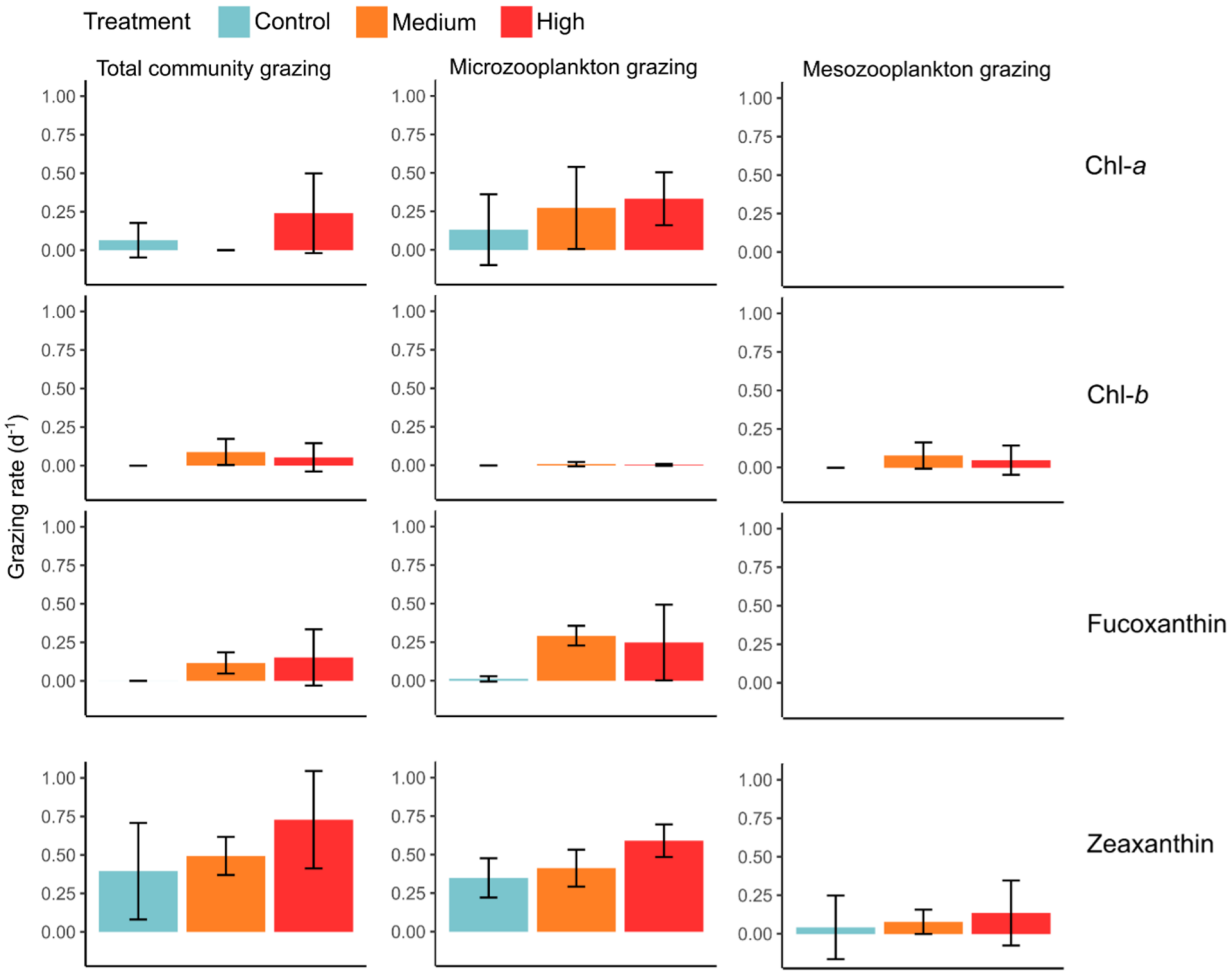

Fig. 6 Total community, micro- and mesozooplankton grazing rates (columns) estimated from pigments concentrations (Chl-*a*, Chl-*b*, Fucoxanthin and Zeaxanthin, rows from top to bottom) in the Control (blue), Medium (orange) and High Noise (red) treatments.

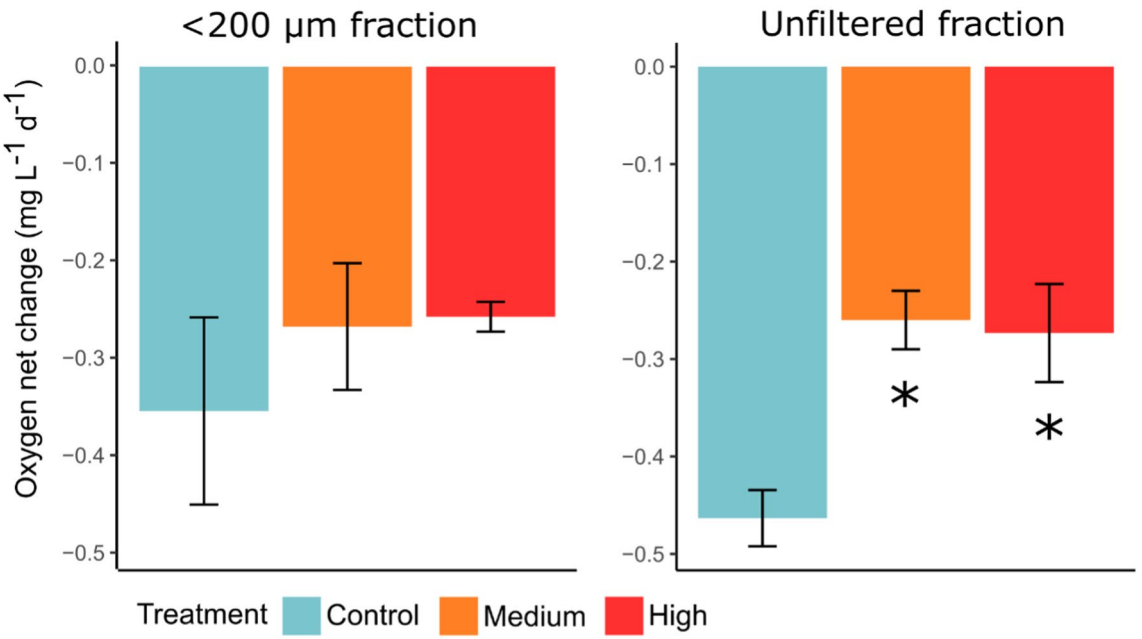

Fig. 7 Daily oxygen net change calculated in the <200 µm fraction (left) and unfiltered (right) in the Control (blue), Medium (orange) and High Noise (red) treatments. Stars (*) indicate a statistically significant difference (at p-value level<0.05) compared to the Control.

Medium Noise treatment, respectively, compared to the Control. As for Chl-*b* and Fucoxanthin, total community grazing rates ranged from 0.05 to 0.15 d^{-1} across the noise treatments, compared to 0.0 d^{-1} in the Control.

Microzooplankton grazing rates were slightly higher in the Control with 0.13 d^{-1} for Chl-*a*, 0.01 d^{-1} for Fucoxanthin, and 0.35 d^{-1} for Zeaxanthin, but were 0 d^{-1} for Chl-*b*. Chl-a rates were 152% and 106% higher, Fucoxanthin rates were 1920% and 2279% higher and Zeaxanthin rates were 69% and 18% higher in the High and Medium Noise treatments respectively, compared to the Control. None of these differences were significant ($p>0.05$).

Finally, the mesozooplankton grazing rates were the lowest, often 0.0 d^{-1}. For Zeaxanthin, the only positive rates were measured in the Control (0.04 d^{-1}) with values 211% and 81% higher in the High and Medium treatment, respectively. Chl-*b* rates ranged from 0.05 to 0.08 d^{-1} in the noise treatments.

Daily net change in oxygen concentrations

In the <200 µm fraction, the daily oxygen net change was -0.35 ± 0.1 mg L^{-1} d^{-1} in the Control, and it was higher but not significantly so in the High and Medium Noise treatments (27% and 25% respectively, Fig. 7. Table 2). In the unfiltered fraction, the daily oxygen net change was significantly higher in the High and Medium Noise treatments, by 41% ($p=0.002$) and 44% ($p=0.001$), respectively, than in the Control (-0.46±0.03 mg L^{-1} d^{-1}).

Discussion

To our knowledge, this study is the first to investigate the effects of OWF low-frequency noise on natural planktonic communities using an in situ experimental setup. We found that phytoplankton growth rates, in particular those based on estimates derived from Chl-*b* and Fucoxanthin concentrations, were significantly higher in the High and Medium Noise treatments compared to the Control.

The trend was consistent across all identified pigments, showing higher growth rates in the High and Medium Noise treatments compared to the Control. This suggests that OWF noise directly and positively affected phytoplankton growth, confirming our first hypothesis that low-frequency noise can directly promote growth rates through physiological stimulation. Our findings align with previous studies reporting that audible sound at 90 dB re 1 µPa, particularly in the low-frequency range (e.g., 80–2200 Hz), stimulated growth in two cultured green algae species (*Picochlorum oklahomensis* and *Dunaliella salina*)[21,31]. Conversely, other studies investigating the effect of pile-driving noise on microalgal physiology demonstrated that low-frequency noise (100–2000 Hz) at a much higher sound pressure level than in the present study (138–170 dB re 1 µPa) increased growth inhibition of different phytoplankton taxa such as diatoms, haptophytes and green algae (*Phaeodactylum tricornutum*, *Isochrysis galbana*, and *Dunaliella tertiolecta*)[32]. While these contrasting results may suggest a sound pressure threshold for negative impacts on plankton physiology, the differences could also come from the difference in sound types, one being continuous noise (OWF) compared to pulse-type noise like pile driving.

Sound, in general, can significantly affect the morphology and physiology of phytoplankton through changes in cell morphology or cell wall characteristics and the electron transfer rate of the cells, directly impacting photosynthetic efficiency and cell growth[32,33]. Though we measured sound pressure instead of particle motion in this study, it is likely that both mechanisms affect the cells by acting as mechanical resonance for the cells[21,34], either promoting or inhibiting metabolic processes depending on the algae's own sensitivity and the frequency and power of the emitted signal. Altogether, this suggests a taxon-specific or sound level-dependent response of microalgae to sound exposure. Indeed, the positive community-level net effect observed in this study does not exclude the possibility that individual species within an assemblage respond differently to sound and that detrimental effects could occur at higher sound levels.

While Chl-*a* is a universal pigment and a robust proxy for estimating phytoplankton biomass and metabolic rate[35,36], growth rates based on pigment concentrations and especially on accessory pigments need to be interpreted with care. Notably, the correlation between pigment concentrations and biomass can be influenced by changes in pigment ratios related to changes in physiology, cell size, or the fact that these pigments can be shared among various phytoplankton taxa. However, the net accumulation of photosynthetic pigments resulting in higher growth rates in the High and Medium Noise treatments reliably indicates an increase in the total physiological activity and productivity of parts of the phytoplankton community. We found a positive, growth-stimulating response in diatoms (represented by Fucoxanthin as a marker) and small green algae (represented by Chl-*b* as a marker). Fucoxanthin was already used as a marker pigment for diatom abundances in Hopavågen[37] and when estimating metabolic rates of diatoms[38,39]. Therefore, the significantly higher growth rates derived from Fucoxanthin estimates in the noise treatments suggest that diatom growth was indeed positively affected by the noise exposure. The same applies to small green algae, as Chl-*b* has been shown to reliably track the growth dynamics of this group[39] notably in Hopavågen[37].

In line with the higher phytoplankton growth rate under noise exposure, the daily net change in oxygen was significantly higher in the High and Medium Noise treatments compared to the Control in the unfiltered fraction community, with a similar trend observed in the < 200 µm fraction. This indicates a significantly reduced net community oxygen consumption under noise exposure. This aligns with the tendency towards higher phytoplankton growth rates observed in the incubations, suggesting increased primary production under noise exposure. The enhanced community-level primary production likely resulted in a more positive net oxygen balance leading to a higher net oxygen accumulation in the noise treatments.

Grazing rates were generally low and not significantly different across treatments. Total community and mesozooplankton grazing rates were overall lower than the microzooplankton grazing rates, indicating that microzooplankton (dominated by small dinoflagellates and ciliates) were the main grazers in the incubation bottles. While few studies reported the effects of anthropogenic noise on metazoans in the plankton[12,19,20,40], its impact on protozoans had not been investigated so far. Thus, our knowledge of the responses of small-sized protozoans such as heterotrophic dinoflagellates or ciliates is very limited.

Our results indicate that while phytoplankton growth rates were significantly impacted over the 22-hour noise exposure, micro- and mesozooplankton grazing activity was not strongly affected. This suggests that noise had a direct and immediate effect on phytoplankton physiology. In contrast, the lack of significant response in zooplankton grazing did not support our second hypothesis of a negative impact of noise exposure via mechanoreceptor disruption. Instead, it may indicate a functional decoupling between phytoplankton and their grazers. Since the dilution method provides independent estimates of growth and grazing rates, the lack in grazing response suggests a time lag in the grazer community response when exposed to noise, while prey availability increased. While direct metabolic shifts occur rapidly in primary producers, indirect effects altering the food web can only be observed over longer time-scales and prolonged exposure. This was notably observed by Rojas et al.[41], who reported a noise-induced trophic cascade in freshwater communities after a longer exposure of several days to boat noise.

Experimental setup advantages and constraints

Laboratory-based experiments addressing the impact of sound on aquatic biota often face physical challenges related to tank constraints[26,27]. While working in situ allowed us to mitigate most of these limitations, this approach also introduced some new challenges. Finding optimal experimental sites to run the Control as well as the Medium and High Noise treatments in parallel was crucial, considering that sound propagates efficiently underwater[42]. Fortunately, the combination of shallow water, soft sediment, and the presence of a sandbank in Hopavågen lagoon, provided sufficient acoustic isolation for the Control site[43,44]. This allowed us to successfully broadcast sound up to 105 dB in the western part (for the Medium and High Noise treatments) while keeping the eastern part (Control) acoustically isolated. This setup, however, implied that the Control and Noise treatments were geographically separated by a few hundred meters and environmental conditions needed to be identical. Temperature, salinity, nutrient concentration, and light availability are key factors influencing planktonic communities[45–47]. In this study, the experimental units were filled with natural seawater, ensuring that initial biotic and abiotic conditions were comparable to the surrounding seawater. The surrounding water also shared similar temperature, salinity, and light characteristics across all sites. The homogeneous salinity and temperature measured in the lagoon during the experiment indicated that the few rainfall events that occurred during the experiment did not significantly alter salinity, suggesting minimal changes in water column turbidity. In addition, due to the high solar angle and long daylengths at this latitude in summertime, light heterogeneity in the lagoon is considered minor. Furthermore, Hopavågen lagoon is not generally affected by significant freshwater inputs[48] that could increase water turbidity and affect light availability. Altogether, these findings confirm that the Hopavågen lagoon was a relatively stable and homogenous water mass, making it a suitable and unique environment for noise experiments, especially during the summer period.

The High Noise treatment during this experiment was equivalent to sound levels commonly recorded at distances approximately 500–1000 m from operating offshore wind farms[24]. We chose these lower, more pervasive levels rather than peak levels emitted by OWFs, as plankton are likely to be exposed longer to such lower levels as they drift through wind parks. Hence, the exposure duration of 22 h to these levels is ecologically realistic. While the speaker emitted sounds above 100 Hz, it could not reproduce the sub-100 Hz frequencies typical of operating OWFs. As a result, the observed effects may not fully reflect the impacts of the real exposure of marine organisms to full-spectrum sound from offshore wind farms. Thus, future studies using a speaker with broader frequency response could explore the effect of lower frequencies, and possibly higher noise levels on planktonic communities.

In conclusion, this bottle incubation experiment, using a novel experimental setup for acoustic exposure studies, provided evidence that exposure to OWF low-frequency noise, specifically within the 100–500 Hz range, can significantly alter key metabolic rates of natural planktonic communities. Performing in situ experiments with highly-dynamic systems such as plankton communities often requires a compromise between obtaining sufficient data to tease out ecologically relevant patterns and being able to conduct proper sampling. In the present

experiment, three replicates per treatment were used, to ensure that all treatments and replicates could be sampled and processed within a reasonable time to prevent exposing differences between treatments and/or replicates related to differences in sampling time. However, this relatively low number of replicates may have limited the statistical power of the analyses. Nevertheless, the present experiment showed that phytoplankton was affected by OWF noise since significant effects on growth rates and the community's net oxygen change were observed, suggesting enhanced primary production under this type of noise exposure. Such noise-induced changes in plankton metabolic rates have the potential to propagate up the food web and induce cascading effects on planktonic communities, thus pointing at the consequences of noise exposure in terms of ecosystem functioning and services in areas occupied by offshore wind farms. Although higher primary productivity could enhance bottom-up energy transfer and biological carbon uptake around offshore wind farms, such shifts could also trigger undesirable trade-offs. The net implications for marine ecosystem services thus remain to be fully quantified.

Materials and methods

Study site

The study was conducted in the lagoon of Hopavågen, located in central Norway close to the mouth of Trondheimsfjord, Trøndelag (Fig. 1). Hopavågen is characterized by deeper water in the northern side with a maximum depth of 31 m[48], while the southern part is relatively shallow with depths between 2 and 10 m and a tidal fluctuation of approximately 2 m. The benthos of the lagoon comprises predominantly soft sediment composed of silt and sand in the southern Section[48,49], while the littoral zones are a rocky intertidal. The lagoon is characterized by a large sandbank on the southern shore dividing the lagoon into an eastern and western part. The lagoon is connected to the outer part of Trondheimsfjord via a small channel. This connection is characterized by strong tidal currents, resulting in a significant water exchange with the adjacent fjord with 11% turnover of the total seawater volume of the lagoon per tidal cycle[49]. Consequently, the planktonic communities within the lagoon are representative of the coastal plankton communities found in the fjord. Hopavågen is a relatively remote site; although a small road borders the southern shore, generating minor road traffic noise, human and marine traffic activities are negligible (e.g., no commercial fishing and only rare encounters of recreational swimming/fishing)[48]. The remote location and the low human activity make the lagoon highly suitable for a controlled noise exposure experiment.

Experimental sound exposure set up

We deployed an underwater speaker (UW30-100 Underwater Loudspeaker, Electro-Voice) on a custom-made wooden support on the southwestern side of Hopavågen, close to the shore, positioned approximately 70 cm above the seafloor in a water column that varies between 2–4 m depth depending on the tides (63°35.556' N; 9°32.442' E). The speaker was connected to a compact amplifier (t.racks dsp 4 channel, Thomann Music) and computer on land. The experimental sound source was a 22-hours-long section of an original recording of underwater wind farm sound, captured at 22 m depth in the Belwind offshore wind park in the North Sea (51°40.580' N; 2°48.650' E). More specifically, the hydrophone was positioned inside the Belwind wind farm, at the center of a square formed by 4 operational wind turbines, with the nearest turbine located 300 m away from the hydrophone.

The raw recording was low pass filtered using a 3rd -order Chebychev filter with cutoff at 1200 Hz to remove sounds not coming primarily from the OWF. A series of playback tests was conducted while broadcasting the wind farm noise from the computer on VLC player, to determine the locations for the treatment and Control sites. We used a calibrated icListen HF hydrophone (Ocean Sonics) deployed at 1 m depth at various locations in the lagoon to evaluate the sound pressure levels (SPL) at different locations. This allowed us to establish three locations with different noise levels (including a Control site), all within a water depth from 2 to 4 m. These locations were positioned between 15 and 420 m from the speaker (Fig. 1). While it was not logistically feasible to have a

speaker playing back no sound closer to the control site, given the relatively long distance between the speaker and even the High Noise treatment location, electromagnetic field (EMF) emitted by the speaker is not a likely reason for observed differences among treatments.

For all three locations, root-mean-square sound pressure levels (SPL_{RMS}) and power spectral densities (PSD) were calculated, over a 50–2400 Hz frequency range. These measurements were computed from a 10-sec-long recording collected at each location during the playback broadcast in calm weather prior to the experiment.

Noise treatments

Using the experimental set up described above, a bottle incubation experiment was conducted in August 2023. The broadcast and experiment started at 17:00 on August 13 and continued until 14:30 on August 14, 2023. The primary goal was to assess the effects of noise exposure on plankton metabolic rates by exposing a natural planktonic community simultaneously to different levels of sound from operational OWF over a 22-hour period.

To monitor the acoustic environment, two SoundTraps (ST 300, Ocean Instruments, New Zealand) were deployed on the seafloor at the Control and High Noise locations. SoundTraps were attached to a concrete block connected to a line and a buoy. They recorded continuously at 48 kHz over the experimental period to monitor the soundscape and ensure that the broadcast noise was not propagating to the Control location. From those recordings, a long-term spectral average, with 1 Hz frequency and 1 s temporal resolution, was computed over the 0–2400 Hz frequency range. In addition, 1-minute SPL_{RMS} for the 50–2400 Hz frequency range was calculated at both locations.

Environmental conditions

Given the spatial separation of the treatment locations, we measured temperature and salinity profiles at each site during both the deployment and retrieval of the incubation bottles using a CastAway CTD to confirm the homogeneity of the environmental conditions across treatments (Supplementary Fig. 1, Supplementary Table 1).

Bottle incubation experiment

To estimate the phytoplankton growth and microzooplankton grazing rates simultaneously but independently, a bottle incubation experiment consisting of a two-point dilution experiment with 100% and 10% dilution levels was conducted[50,51], using the <200 µm size fraction of the natural plankton community (referred to as **<200 µm fraction)**. We could not directly measure sound pressure levels inside the bottles during the experiments. However, the same bottles were used for all treatments, therefore any potential bottle effect on sound propagation was the same across the treatments and thus would not be a factor explaining any differences among the treatments. An initial assessment of the zooplankton composition revealed that the community was predominantly composed of copepodites and meroplankton larvae of relatively small size (see Supplementary Fig. 2), with a notable absence of large predators. Given this specific community size-structure, we added another dilution level of 100% unfiltered seawater (hereafter the **unfiltered fraction**) as a proxy to capture the grazing pressure from the total community. Grazing rates by mesozooplankton **(>200 µm fraction**) could then be derived from the difference between the filtered and unfiltered fraction.

To conduct the dilution experiment, natural seawater was collected from a shallow part of Hopavågen at ca. 1 m depth, accessible by foot during high tide, enabling the filling of 20 L carboys with 86 mm opening by immersion. The collected seawater was poured and pooled into two 100 L containers. One container was covered with a 200 µm mesh to remove mesozooplankton grazers during the pouring, thus constituting the <200 µm fraction for the dilution experiment. The second container was filled without pre-filtration thus comprising the unfiltered fraction, including both micro- and mesozooplankton. A portion of this unfiltered seawater was then filtered using a gravity-cartridge filter (Polycap 0.8–0.2 µm) to obtain filtered seawater to set up the dilution levels[50,51].

Triplicate transparent 2.4 L polycarbonate bottles were filled according to the following dilution levels: (1) **10% <200 µm fraction (**10% of the <200 µm fraction and 90% filtered seawater, (2) **100% <200 µm fraction (**only microzooplankton grazers) and (3) **100% unfiltered fraction** (Micro- and mesozooplankton grazers). To assess potential nutrient limitation, (4) **100% <200 µm fraction + nutrient** was amended with 2mL of f/2 medium[52] per bottle, for comparisons with the 100% <200 µm fraction (non-amended) level. Each bottle was filled to the top and a plastic film was applied to the opening, to prevent air bubbles, before tightly sealing with the bottle cap. Bottles were then deployed in situ on a rope at 1 m depth. They were incubated for a 22-hours instead of the standard 24 h due to logistical constraints, though still capturing a full day-night cycle.

Before incubation, triplicate seawater samples (1–2 L) were collected from the pooled 100% <200 µm and 100% unfiltered fraction containers. These initial samples served as the reference for all corresponding dilution levels (10% <200 µm fraction and 100% <200 µm fraction + nutrient). After the incubation period, samples were collected from every individual bottle. All samples were then filtered onto glass fiber GF/F filters (0.7 µm pore size) using a water pump in a light-attenuated room. Filters were then folded into cryotubes, flash-frozen in liquid nitrogen, and stored at − 80 °C for later pigment analysis.

Pigment analyses

Pigment composition and concentrations, serving as a proxies for phytoplankton functional groups, were measured with High Performance Liquid Chromatography (HPLC, Hewlett Packard 1100) using the method of Summers et al.[53]. Briefly, pigments were extracted in 100% methanol at -20 °C for 24 h. Extracts were analyzed within 24 h and pigments identified based on retention time and spectrum, following Roy et al.[30].

Zooplankton identification and counting

The initial micro- and mesozooplankton community was sampled to obtain a comprehensive overview of the entire planktonic community and its different size fractions.

Metazoans were analyzed from a 10 L sample taken from the unfiltered fraction. This sample was concentrated over a 20 µm mesh, transferred to a polycarbonate sample bottle, fixed with borax-buffered formaldehyde (4% final concentration) counted/identified using a binocular microscope (Leica M205 C).

Protozoans were analyzed from three 200 mL subsamples of the <200 µm fraction fixed with acidic Lugol's iodine solution (2% final concentration). The samples were analyzed under an inverted microscope (Zeiss Vert. A1) using the Utermöhl technique[54] and cell sizes and taxonomic composition assessed[55].

Growth and grazing rate estimation

Both growth and grazing rates were estimated based on changes in pigment concentrations during the dilution experiment. Therefore, growth rates for respective phytoplankton groups were estimated for each measured pigment. Further, micro- and mesozooplankton grazing rates were calculated to assess the consumption of these phytoplankton groups based on the corresponding pigment changes.

For this purpose, instantaneous growth rates (k) were estimated for all dilution levels (10%, 100% <200 µm, and 100% unfiltered fractions) using the equation from Calbet & Landry[56]:

$$k = \frac{1}{t} \times \ln\left(\frac{N_{t22}}{N_{t0}}\right)$$

Where k is the instantaneous growth rate (d^{-1}), t is the incubation time in days, and $Nt_{(0)}$ and $Nt_{(2^2)}$ represent the relative biomass concentrations at the start and end of the incubation, respectively (corresponding to the pigment concentrations in the present study[39,57]). Phytoplankton growth rates were considered equal to $k_{10\%}$[50]. However,

as the dilution level 10% was not nutrient-amended, these rates do not represent maximal growth rates[50,56], but rather natural growth rates that better reflect the natural metabolic rates of the given plankton community[58,59].

Microzooplankton grazing rates were estimated as the difference between $k_{10\%}$ and $k_{100\%\ <200\ \mu m\ fraction}$. **Total community grazing rates** were calculated as the difference between $k_{10\%}$ and $k_{100\%\ unfiltered\ fraction}$. **Mesozooplankton grazing rates** were derived by subtracting $k_{100\%\ <200\ \mu m\ fraction}$ from $k_{100\%\ unfiltered\ fraction}$. In cases where microzooplankton, total community or mesozooplankton grazing rates were negative, they were set to 0.00 d^{-1}, as negative grazing has no biological significance[56].

Daily net change in oxygen concentration

Measurements of change in dissolved oxygen concentrations were conducted simultaneously with the dilution experiments in separate bottles to ensure high-precision measurements and limited bottle manipulation. Two sets of triplicate polycarbonate bottles (72 mL) were filled, one with the <200 µm fraction, and the second with the unfiltered fraction, allowing the distinction between micro- and mesozooplankton oxygen net change. Bottles were filled carefully to minimize the formation of air bubbles, and the water was left to settle for 20 min prior to initial oxygen concentration measurements. Thereafter, each bottle was topped up with its respective water size-fraction, covered with a plastic film to prevent air exchange and bubbles, sealed tightly with a cap and secured upright in a plastic basket. To ensure exposure consistency, these bottles were also deployed at 1 m depth in the water column for 22-hours. After incubation, the bottles were gently retrieved and carefully opened to measure final oxygen concentrations. Measurements were performed using a stainless-steel probe (FOSPOR matrix coated with black medical grade silicone for stray light protection, 3/16") connected to a Neofox sensor platform (Ocean optics).

The daily net change in oxygen concentration was then calculated as:

$$Daily\ net\ change = \frac{1}{t} \times (C_{t24} - C_{t0})$$

Where t is the incubation time in days, and C_{t0} and C_{t24} are the oxygen concentrations measured before and after incubation, respectively.

Statistical analyses

The statistical analyses were conducted with R 4.5.0. To identify the effects of the noise treatments on growth rates, grazing rates (for total community, micro- and mesozooplankton), and oxygen net change, values measured in the Medium and High Noise treatments were compared to those of the Control treatment. An Analysis of Variance (ANOVA) was applied to each dataset, with treatment as a fixed factor. If the model's residuals were confirmed to follow a normal distribution, a post-hoc Tukey test was performed to determine the statistical differences between treatments. If the assumption of normality was not met, which was the case for Zeaxanthin in the microzooplankton grazing rate analysis, a Kruskal-Wallis test was used instead, followed by a pairwise Wilcoxon rank-sum test with a Benjamini-Hochberg (BH) correction applied. To assess the potential significant difference in growth rates estimated without and with nutrient addition, a Kruskal-Wallis test was performed for each pigment and for each treatment individually. Subsequently, a BH correction was applied again to account for multiple comparisons and minimize the risk of a Type I error.

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Author contributions JC, AŠ and NA designed the experiment. JC, TS, ER and AŠ performed the experiment. JC and TS analyzed the pigment samples and JC the zooplankton samples. AN provided the sound files. JC wrote the original draft with the input of all co-authors. All authors contributed to the article and approved the submitted version.

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Data availability The data that support the findings of this study are available from the corresponding author upon request. They will soon be openly available in a repository.

Declarations

Competing interests The authors declare no competing interests.

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