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Blue Mussels (*Mytilus edulis*) Improve Light Conditions in a Downstream Eelgrass (*Zostera marina*) Meadow in the Limfjorden, Denmark

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Abstract

Eelgrass (*Zostera marina*) constitutes critical habitat worldwide in terms of ecosystem services and biodiversity, yet less than 30% coverage remains in Danish waters compared to historical records. Persistent eutrophication has substantially reduced water clarity, making light the primary limiting factor for the distribution of eelgrass. Through particle filtration, filter-feeders such as blue mussels (*Mytilus edulis*) can influence light conditions in coastal habitats. This study hypothesized that blue mussel beds could improve light conditions within nearby eelgrass meadows and thus facilitate eelgrass growth. Light and current data were gathered from 37 sampling stations in three different habitats (eelgrass meadows, blue mussel beds, and mixed) at two sites in a shallow estuary in the Limfjorden, Denmark, characterized by different mussel–eelgrass configurations from May to September 2023. Across the three habitats, the light attenuation coefficient for photosynthetically active radiation, K_d(PAR), was generally lower above blue mussel beds compared to eelgrass meadows and mixed habitats, likely due to suspended particle filtration by the mussels. Further supporting that mussels improved light conditions, median K_d(PAR) in the eelgrass was lower when the eelgrass meadows were downstream from the mussel beds, than for the opposite current direction. Using state-space models, temporal changes in K_d(PAR) were shown to be predominantly controlled by seasonal changes in chlorophyll *a* concentration in Lovns Broad, whereas current velocity only had minor impact. These findings suggest that blue mussels can improve water clarity in adjacent eelgrass meadows, likely alleviating light limitation and thereby supporting eelgrass growth and ecosystem functioning.

Keywords Benthic light · Biogenic habitats · Coastal habitats · Facilitative effects · Light attenuation · State-space models

Introduction

Aquatic vegetated habitats are experiencing rapid decline resulting in significant worldwide losses of both spatial extent and biodiversity (Lotze et al., 2006; Orth et al., 2006: Dunic et al., 2021). In Danish waters, eelgrass (*Zostera marina*) has suffered dramatic reductions in coverage, with less than 30% remaining compared to historical records (pre 1930 s), primarily due to eutrophication-driven declines in water clarity (Staehr et al., 2019; Dunic et al., 2021; Lange et al., 2022). Light availability is widely recognized as the primary factor limiting eelgrass distribution and recovery (Krause-Jensen et al., 2011). Similar to eelgrass, blue mussels (*Mytilus edulis*) are considered a foundational species in coastal waters and can regulate light availability in waters within and adjacent to mussel beds by locally removing suspended particles through filter feeding (Petersen et al., 1997; Dolmer, 2000; Riemann et al., 2016). Dolmer (2000) found that vertical profiles of phytoplankton decreased toward mussel beds in Limfjorden, highlighting their filtration activity. Because suspension-feeding bivalves and

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seagrasses frequently co-occur (Peterson et al., 1984) in Danish coastal habitats, their interactions may generate facilitative effects, with mussel beds potentially enhancing light conditions for adjacent eelgrass meadows.

Previous studies, both laboratory and in-situ experiments, suggest that blue mussels (*Mytilus edulis*) may facilitate eelgrass growth and survival by locally reducing water column turbidity, hydrodynamic stress, and by fertilizing the sediment porewater with ammonium and phosphate within the mussel bed (Reusch et al., 1994; Riisgaard et al., 2004; Bos & van Katwijk, 2007; Wall et al., 2008; Gagnon et al., 2021). The improved water clarity can benefit near-bottom phototropic organisms such as eelgrass. Reciprocally, eelgrass can facilitate the survival and growth of blue mussels by reducing the flow of water above the mussel bed, thus improving food supply, larvae settlement, and providing physical protection (Petersen et al., 1997; Bos & van Katwijk, 2007; Gagnon et al., 2021). Transplantation of eelgrass alongside suspension-feeding marine bivalves, such as blue mussels, has previously been shown to enhance ecosystem functions that benefit both species (Bos & van Katwijk, 2007; Pajusalu et al., 2023), particularly through the reduction of hydrodynamic exposure as a synergistic benefit (Petersen et al., 1997; Bos & van Katwijk, 2007; Gagnon et al., 2021). Meanwhile, the impact of mussel filtration on improving water clarity outside the mussel bed in natural field settings remains understudied. To our knowledge, no studies have yet focused on how mussel filtration affects light conditions in eelgrass in a natural ecosystem.

Eelgrass is a key species in coastal and estuarine ecosystems and an indicator species in the European Union Water Framework Directive (WFD). It provides numerous important ecological services such as carbon uptake and nutrient cycling, wave damping, water clarity enhancement through sediment stabilization, and increased sedimentation of particles, as well as enhanced biodiversity of associated marine communities through shelter provision and foraging possibilities (Cullen-Unsworth et al., 2013; Nordlund et al., 2016; Orth et al., 2020; Lange et al., 2022). Blue mussels are also a keystone species in the Limfjorden valued both commercially and for their ecosystem services. Blue mussels contribute to sediment stabilization, serve as a food source for higher trophic levels, improve water clarity through filtration, and provide habitat for other species (Dolmer, 2000; Wiles et al., 2006; Wall et al., 2008; Beyer et al., 2017; Steeves et al., 2022). The shallow Danish fjord, the Limfjorden, which connects the North Sea with the Kattegat, was fringed with belts of eelgrass extending to depths of 8 m prior to the 1930 s (Krause-Jensen & Rasmussen, 2009). In Lovns Broad, which is part of a Natura 2000 protected area in the Limfjorden, the current estimated depth limit for eelgrass is reduced to only 2 m (Nielsen et al., 2023), compared to 5.5 m historically (Krause-Jensen & Rasmussen, 2009). Most of the Limfjorden system, including Lovns Broad, is currently classified as having "Bad ecological status" (Ministry of Green Transition, 2024), which is the lowest classification under the WFD reflecting the ecological challenges and significant ecological degradation in this fjord-system.

This study was implemented to investigate the potential facilitative effect of blue mussels on eelgrass conditions by addressing the question: How does mussel filtration affect light conditions in an adjacent shallow eelgrass meadow? We investigated this by monitoring the light attenuation coefficient for photosynthetically active radiation, K_d(PAR), water quality and current velocity over the eelgrass growth period for two sites with differing mussel-eelgrass configurations in Lovns Broad in the Limfjorden, Denmark. The aim was to advance knowledge of facilitative effects between eelgrass and mussels and to better understand the nature of their co-existence in natural coastal systems.

Materials and Methods

Study Area Description and Habitat Characterization

The study area was located in Lovns Broad, in the southeastern part of the Limfjorden, Denmark (Fig. 1a and b). The Limfjorden is the largest fjord system in Denmark, with a catchment area of 7670 km^2 and a coastline of more than 1000 km (Dolmer, 2000). It is a micro-tidal, shallow estuary with a maximum variation in tides up to 0.2 m (Wiles et al., 2006) and consists of several smaller basins connected by narrow straits, with Lovns Broad located centrally in the fjord system. The Limfjorden receives cold saline water from the North Sea in the west, and the overall water flow is eastward, towards the Kattegat (Dolmer, 2000). The fjord system is heavily impacted by nutrient runoff from agriculture in the catchment area, and experiences seasonal anoxia (Hofmeister et al., 2009; Hansen & Rytter, 2024). Due to the eutrophic conditions in the Limfjorden, light is often the limiting factor for submerged vegetation (Krause-Jensen et al., 2011). In Lovns Broad, water circulation is predominantly controlled by longshore currents (Erichsen & Birkeland, 2019). Limited water exchange between Lovns Broad and adjacent waters results in this area seasonally experiencing some of the most persistent and severe oxygen depletion in the Limfjorden, where fish mortality events are often observed (Hansen & Rytter, 2024).

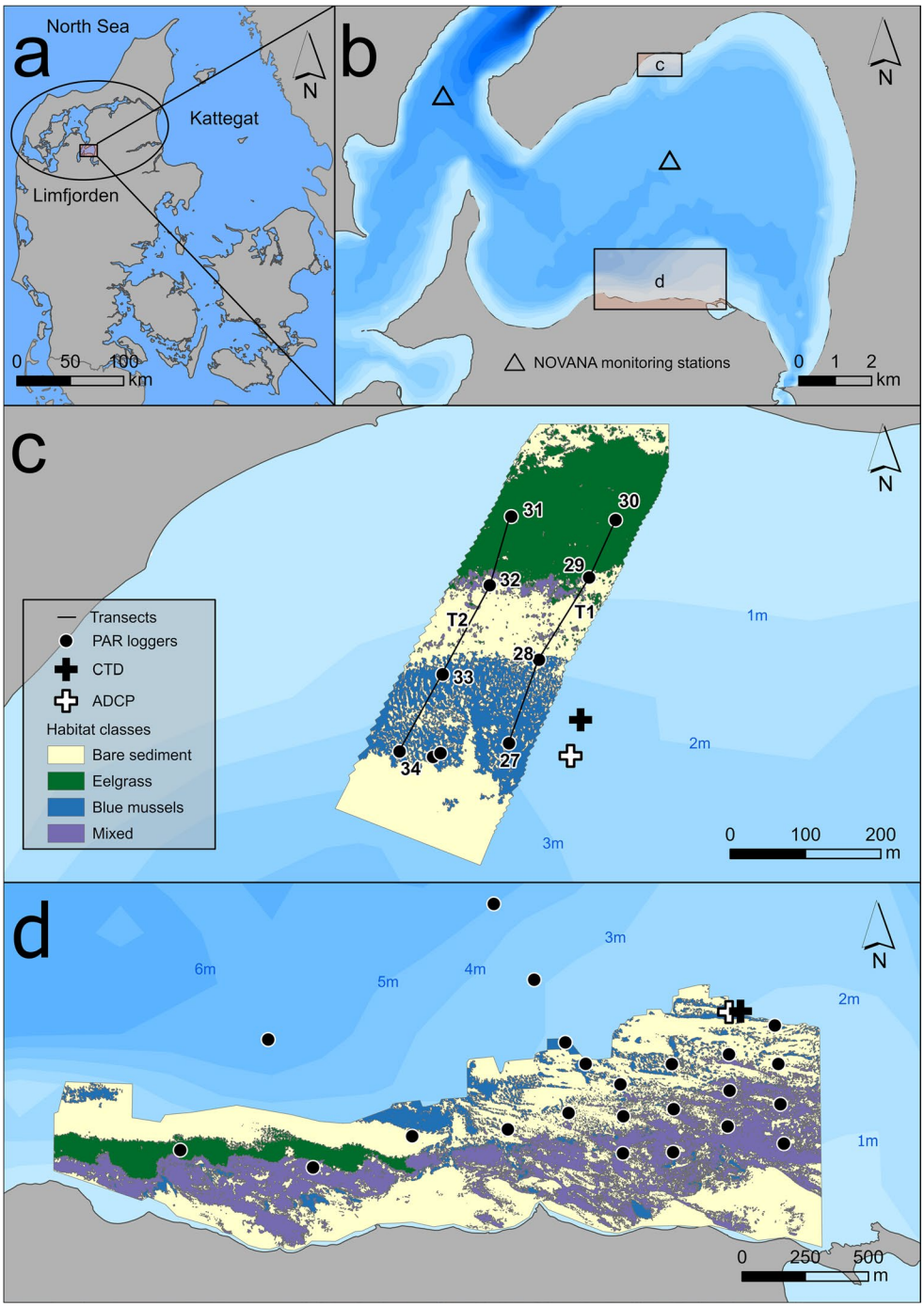


Fig. 1 The study area Lovns Broad situated in the Limfjorden in Denmark (**a**). The field study comprised of a northern and southern site in Lovns Broad (**b**). Field data collected at both the northern (**c**) and southern (**d**) sites included photosynthetically active radiation (PAR), conductivity, temperature and depth (CTD) and current measurements (ADCP) with sensors deployed at multiple locations at varying water depths and four habitat classes

Two study sites in Lovns Broad were selected based on different mussel-eelgrass habitat configurations identified in UAV-based habitat surveys following the methodologies outlined in Thomasberger et al. (2023) and Thomasberger and Nielsen (2023). The two study sites were categorized into three habitat classes based on the dominating coverage: eelgrass meadows, blue mussel beds, and mixed habitats (Fig. 2). The two study sites comprised of a northern site with bands of eelgrass and blue mussels separated by mostly bare sediment situated parallel to the shoreline (Fig. 1c). The southern site was dominated by patches of mixed blue mussel and eelgrass (Fig. 1d). The habitat configurations at both sites appear to be stable as orthophotos going back to 1999 show similar coverage, though varying densities, of both eelgrass meadows and mussel beds (see Online resource 1, Fig. S1 & S2).

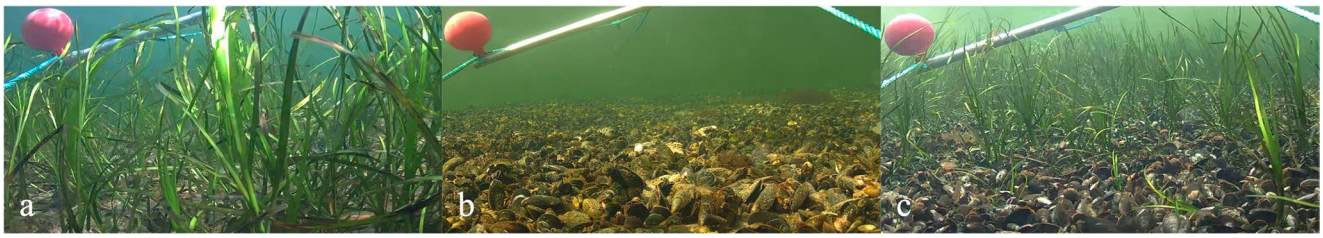


Fig. 2 Screenshots taken from vessel-based video recordings from May 2022 of eelgrass (**a**), blue mussels (**b**) and a mixed habitat (**c**). The red buoy was attached to add buoyancy to the sled to avoid plowing through the sediment

Photosynthetically Active Radiation and Light Attenuation Coefficient

Measurements of photosynthetically active radiation (PAR) were collected continuously from May to September 2023 at a total of 33 fixed stations using identical flat (2π) Odyssey Xtreme PAR loggers (Dataflow Systems Ltd., Christchurch, New Zealand). All sensors were mounted upright on frames 0.5 m above the seafloor in relatively open areas within the habitats and recorded PAR in 5-minute averaged ensembles. The distance from the seafloor minimized the potential effect of eelgrass shading and the benthic boundary layer caused by mussel filtration. All PAR loggers were coated in antifouling paint and calibrated prior to deployment. To ensure continuous measurement accuracy, all sensors were cleaned for biofouling every 1–3 weeks to remove drifting seaweed, settling of fine particles and formation of biofilm (Carruthers et al., 2001). Post data collection, the measurements were visually investigated before and after cleaning and only neglectable differences in PAR were detected. Of the 33 stations, 10 were located at the northern site and 23 at the southern site (Fig. 1c). At the northern site, the stations located in the eelgrass had a mean depth of 0.8 m, and the stations located in the mussels had a mean depth of 2.4 m. The stations located in the mixed habitat in the south had a mean depth of 1 m. Stations at both sites were arranged in a modified grid pattern constrained by local bathymetry. At both study sites, additional reference PAR loggers were placed at the surface. Each PAR station was ascribed to a habitat class based on the dominating habitat within a radius of 10 m. This was to account for both GPS uncertainties (5–8 m) and the known spatial influence of e.g., blue mussels, where the phytoplankton depletion layer extends beyond the edge of the habitat (Saurel et al., 2013). Although multiple habitat types occur at the southern site, only stations located within mixed-habitat areas were included in this study, in order to compare with discrete habitats in the north.

Continuous records of water depth for each PAR logger were obtained by calculating the difference in the initial water surface elevation, the height of the sensor face, and the fluctuating water surface elevation over time. The latter was independently retrieved for each study site with collocated HOBO water level data loggers (Onset Computer Corporation, Bourne, MA, USA).

K_d(PAR) was calculated using Beer-Lambert Law as:

$$K_d\,(PAR) = -\frac{\ln\left(\frac{I_{z2}}{I_{z1}}\right)}{z_2 - z_1} \quad (1)$$

where I_{z2} [µmol m^{-2} s^{-1}] is the irradiance at depth z_2 [m] (the station sensor) and I_{z1} [µmol m^{-2} s^{-1}] is the irradiance at depth z_1 [m] (the reference sensor in the water surface). A high K_d(PAR) implies a high light attenuation through the water column and therefore low availability of PAR at depth. Light attenuation is principally affected by colored dissolved organic matter, phytoplankton, and inorganic particulate matter (Markager, 2004; Wen et al., 2018). Chlorophyll *a* data were complemented with measurements from NOVANA (the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment) from Skive Fjord and Lovns Broad monitoring stations during 2023. Calculation of K_d(PAR) based on measurements of PAR at only two depths can potentially overlook stratified layers in the water column. Although parts of the Limfjorden are periodically stratified (Wiles et al., 2006; Hofmeister et al., 2009), this effect is expected to have minor influence due to the shallow depth, and therefore likely mixed water column.

Acoustic Doppler Current Profiler

For each site, current velocity and direction were measured with acoustic Doppler current profilers (ADCP). The northern ADCP was a Teledyne Sentinel II Workhorse 600 kHz (Teledyne RD Instruments, Poway, CA, USA) placed ~0.75 m above the seafloor in water of ~2.5 m depth, facing upwards. The southern ADCP was a Nortek Signature 1000 (Nortek, Rud, Norway) placed ~0.25 m below the water surface in water of ~2 m depth, facing downwards. Velocities

were averaged in 5-minute ensembles from May to September. The mean current direction was estimated after smoothing it, using a rolling window function (rollapply; Zeileis & Grothendieck, 2005, R Core Team, 2025) in RStudio (Version 4.4.2) to impute less weight to sudden extreme variations. A sensitivity analysis with different window sizes (15 to 100 min) was carried out, and the smoothed data were visually inspected. A window size of 30 min (equal to six time steps) was chosen as a compromise between smoothing the data and still including the hourly and daily variation in current direction. For the northern site, to assess the interaction between mussels and eelgrass, data was extracted for times when water was either flowing from mussel-to-eelgrass, or from eelgrass-to-mussel (Fig. 1c). The mussel-to-eelgrass direction was defined as currents going from a range of 155° −245° (southwest) towards a range of 335° −65° (northeast), while the opposite direction (northeast towards southwest) was defined as the eelgrass-to-mussel direction.

Measurements from the ADCP stations were assumed to be representative of their respective sites. Although only one ADCP was deployed per site, a local 3D hydrodynamic model for the Limfjorden (Erichsen & Birkeland, 2019) shows dominant longshore currents with limited directional variability within both the northern and southern sites, indicating that a single station adequately captures site-specific current conditions in Lovns Broad.

The Concept of Tracking Parcels of Water Between Habitats

To investigate how filtration by blue mussels and water flow regulate light conditions between habitats, we tracked changes in light experienced by the same parcel of water as it moved between mussel beds and eelgrass meadows. This approach allowed us to distinguish habitat-driven changes in light conditions from spatial variability associated with different water masses. Transect lines were established between blue mussel beds and eelgrass meadows to follow changes in light conditions along the direction of water flow. At the northern site, two parallel transects were placed perpendicular to the belts of blue mussels and eelgrass. Each transect consisted of four stations (stations 27–30 and 31–34), and all stations were equipped with PAR loggers (Fig. 1c). Water flow data were obtained from a single ADCP station at each site. Water parcels were tracked along the transects by accounting for the time required for a parcel to travel between stations, based on the mean current velocity and distance between stations. For example, a parcel of water at station 27 at time t_0 was compared to the same parcel at station 28 at time $t_0 + \Delta t$. The longest periods of consecutive mussel-to-eelgrass and eelgrass-to-mussel flow were approximately 2 h, occurring on 4 May 2023 and 3 June 2023, respectively, and were selected for further analysis. Confidence intervals were created using bootstrapping to avoid reliance on asymptotic behavior, as the data violated assumptions of normality and sample size required by standard parametric methods.

Statistical Analyses

Differences in K_d(PAR) among habitats were detected using a Kruskal-Wallis test, followed by a post hoc Dunn test for multiple comparison. The assumption of normality was assessed using a Kolmogorov-Smirnov test or a Shapiro-Wilk test. Homogeneity of variance was checked applying a Levene's test. Periods of consecutive current direction were compared either by Student's t-test, Welch's t-test or Mann-Whitney U test at a Bonferroni-adjusted significance level, depending on whether the assumptions of normality and homogeneity of variance were met.

We used a state-space model to test whether K_d(PAR) was influenced by chlorophyll *a* and current velocity while accounting for uncertainty due to missing values of the covariates. Before model fitting, we calculated average daily K_d(PAR) from sunrise to sunset and current velocity to match the timescale of the available chlorophyll *a* data and to remove daily noise. This gave us 1178 observations of K_d(PAR) (from nine PAR stations), 127 of current velocity (from the northern ADCP), and 10 of chlorophyll *a* (from two stations). Specifically, daily log(K_d(PAR)) at each station s on each day d was modeled as the response variable with fixed effects of habitat type (categorical: eelgrass versus mussels), velocity, and log(chlorophyll *a*) in the following formula:

$$log\left(Kd_{s,d}\right) = \beta_{0} + \beta_{mussel} + \beta_{Chl} * log\left(\widehat{Chl_{s,d}}\right) + \beta_{speed} * \widehat{speed}_{s,d} + \epsilon_{s} + \alpha_{s,d}$$

Here, β_0 is an overall intercept, β_{mussel} is a contrast of how mussel habitat differs from eelgrass habitat, β_{Chl} is a coefficient for the continuous effect of $log\left(Chl\right)$, and β_{speed} is a coefficient for the continuous effect of speed. The term ϵ_s is a random effect of station which is independent and identically distributed $N\left(0, \sigma_s^2\right)$ to account for repeated measures. The effect of chlorophyll *a* was fit on the log-scale to estimate a power-law relationship of K_d(PAR) with chlorophyll *a* (Morel & Maritorena, 2001). The residual error $\alpha_{s,d}$ is assumed to be normally distributed with mean 0 which makes K_d(PAR) lognormally distributed.

Chl and current speed in the above model are not the observed values, but instead they are the estimated values from the following random walk models, used to fill in the missing values with uncertainty (Auger-Méthé et al., 2021):

$$log\left(\widehat{Chl_{s,d}}\right) = log\left(\widehat{Chl_{s,d-1}}\right) + \eta_{Chl,s,d}$$
$$\text{with } \eta_{Chl} \sim N\left(0, \phi^2_{Chl}\right) \text{ and}$$

$$\log\left(\widehat{speed_{s,d}}\right) = \log\left(\widehat{speed_{s,d-1}}\right)$$
$$+\eta_{speed,s,d} \text{ with } \eta_{speed} \sim N\left(0, \phi^2_{speed}\right)$$

Then the state-space formulation assumes that the observations are normally distributed around the estimates with variance σ^2_{Chl} and σ^2_{speed} (respectively) as follows:

$$log\left(Chl\right) \sim N\left(log\left(\widehat{Chl}\right), \sigma^2_{Chl}\right) and$$

$$log\left(speed\right) \sim N\left(log\left(\widehat{speed}\right), \sigma^2_{speed}\right)$$

These process and observation models were combined in the joint negative log-likelihood. The reason why the state-space approach is preferred over imputing the missing covariates and then modelling K_d(PAR) is that this method includes uncertainty about the missing covariates (Nakagawa, 2015). We used AICc (corrected for small sample size) to compare the full Kd model to all submodels by setting some coefficients (β_{mussel}, β_{speed}, or β_{Chl}) to zero instead of estimating them. While there can be complexities of using information criteria such as AICc on state-space models due to counting random effects, all of our submodels contained the same random effects, so their count was inconsequential (Auger-Méthé et al., 2021).

The models were fit using the package `RTMB` version 1.6 in `R` version 4.4.3 (Kristensen et al., 2016; Kristensen, 2024; R Core Team, 2025) and residuals were checked for model validation (Thygesen et al., 2017). Random effects were estimated using the Laplace approximation. Code for the model and sub models, and data is available in the data repository linked at the end of the paper. Further model details can be found in Online resource 1.

Results

Water Current Direction and Velocity

The water current direction was dominated by westward currents in the northern site (Fig. 3a). In the southern site, the water current direction was dominated by eastward currents, indicating an overall longshore circulation in Lovns Broad (Fig. 3b), which was also confirmed by a local 3D hydrodynamic model for the Limfjorden (Erichsen & Birkeland, 2019). The total number of observations (in 5-minute ensembles) were approximately 40,000, corresponding roughly to 139 days. The darkgrey bars indicate the mussel-to-eelgrass direction (335° −65°), which represents 12.5% of the data, and eelgrass-to-mussel direction (155° −245°), which represents 11.5% of the data.

Light Attenuation Above Eelgrass Meadows and Blue Mussel Beds

When considering each habitat class, the median light attenuation coefficient, K_d(PAR), was lower above blue mussels (0.90 m^{-1}) compared to the mixed habitats (1.26 m^{-1}) ($p<0.001$), both of which were lower than eelgrass meadows (1.29 m^{-1}) ($p<0.001$ and $p<0.001$ Fig. 4).

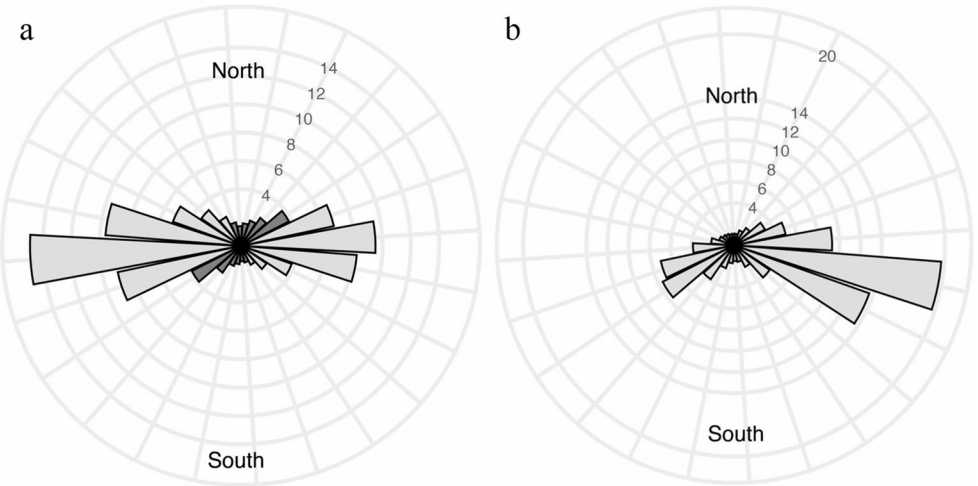


Fig. 3 The occurrence (in %) of water current direction in directional categories during May to September 2023 at the northern site (**a**) and southern site (**b**) in Lovns Broad. The darkgrey bars on (**a**) shows the mussel-to-eelgrass direction (towards 335° - 65°) and eelgrass-to-mussel direction (towards 155° - 245°). The mean current velocity measured in the northern site was 0.084 m s^{-1}, with 80% of the observations in the range between 0.024 m s^{-1} to 0.157 m s^{-1}

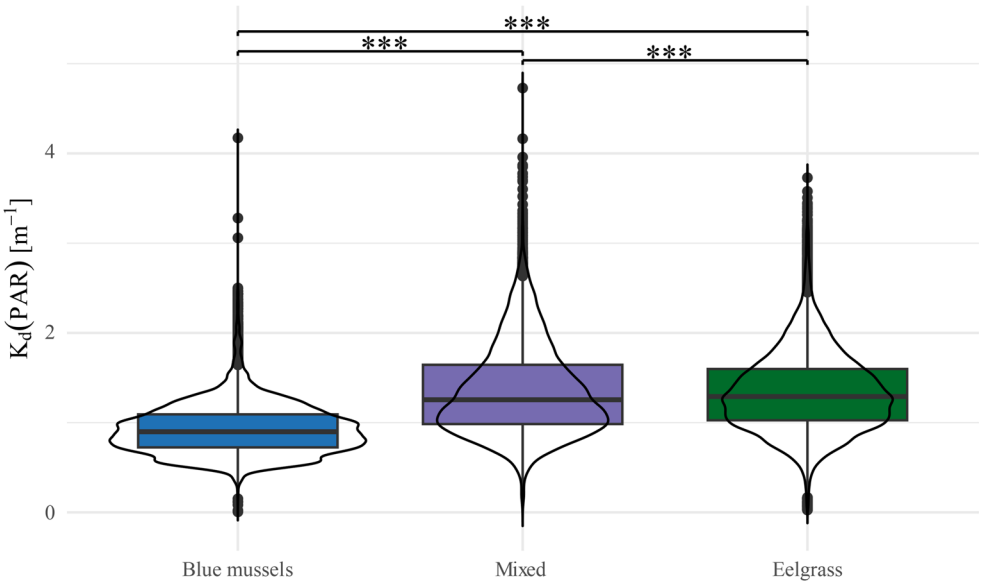


Fig. 4 K_d(PAR) above blue mussels (four stations in the northern site), mixed habitats (11 stations in the southern site) and eelgrass meadows (four stations in the northern site). Violin plots combine box plots and density plots (the distribution of data). The box plots show the median and the interquartile range (IQR), indicating the range between the first quartile (Q1) and the third quartile (Q3). Extreme observations (black dots) are defined based on the IQR as measurements that fall below Q1 − 1.5 · IQR or above Q3 + 1.5 · IQR. *** indicates statistically significant differences at $p < 0.001$

Light Attenuation in Parcels of Water Moving Between Habitats

The light attenuation coefficient, K_d(PAR), was analyzed in parcels of water moving in two current directions, mussel-to-eelgrass and eelgrass-to-mussel. During the longest consecutive period, the currents were oriented from mussels-to-eelgrass for 220 min. After accounting for the time required for water to flow between habitats, this corresponds to a 50-minute period during which filtered water reached the eelgrass. During the longest consecutive period, the currents were oriented from eelgrass-to-mussels for 245 min. After accounting for the time required for water to flow between habitats, this corresponds to a 55-minute period during which eelgrass water reached the mussels.

For both current directions, K_d(PAR) was higher in the eelgrass compared to in the mussel habitat (Fig. 5; Table 1). However, when tracking a water parcel in either direction, the change in median K_d(PAR) was less when currents were flowing from mussel-to-eelgrass than the opposite. As a result, median K_d(PAR) above the eelgrass meadows was lower when the current was flowing from mussel-to-eelgrass compared to eelgrass-to-mussel (Fig. 5; Table 1).

Temporal Drivers of Light Attenuation

To assess current velocity and chlorophyll *a* as temporal drivers of light attenuation, state-space models were constructed. Among the fitted models, the full model had the lowest AICc. Compared to the full model, omitting current

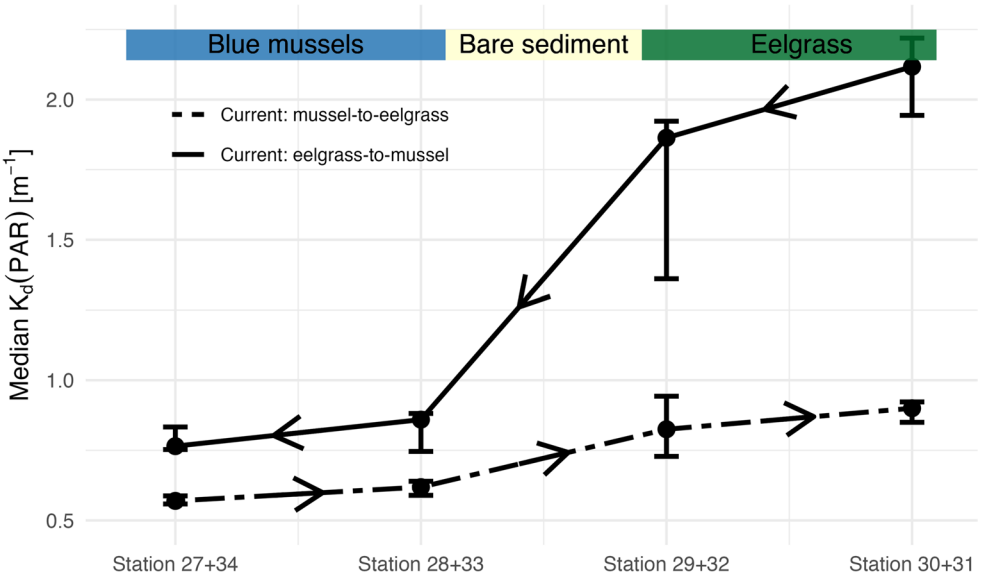


Fig. 5 Median K_d(PAR) measurements along the two transects (Fig. 1c) during the longest consecutive period of mussel-to-eelgrass current (dashed) and eelgrass-to-mussel current (solid). The error bars indicate the 95% confidence interval for each median estimated with bootstrapping based on 1000 resamples. The width of the colored boxes with the habitat names represent the geographical extent of the three habitats along the transects: blue mussels (blue), bare sediment (yellow) and eelgrass (green)

Table 1 Comparison of K_d(PAR) when tracking water parcels across different stations during mussel-to-eelgrass (M-E) and eelgrass-to-mussel (E-M) currents. Bonferroni-adjusted significance level, $\alpha = 0.0125$. *P*-values were derived from statistical comparisons of K_d(PAR) measured in the two directions. The difference in % refers to the difference between station 27+34 and the other stations

Stations	27+34		28+33		29+32		30+31	
Habitat	Mussels		Mussels		Eelgrass		Eelgrass	
Direction	M➔E	E➔M	M➔E	E➔M	M➔E	E➔M	M➔E	E➔M
Median K_d (PAR) [m^{-1}]	0.57	0.76	0.62	0.86	0.83	1.86	0.90	2.12
P-value	$9.8 \cdot 10^{-11}$		$3.8 \cdot 10^{-7}$		$3.8 \cdot 10^{-7}$		$5.5 \cdot 10^{-13}$	
% difference between station 27+34 and other stations	100	100	108	112	144	243	158	276

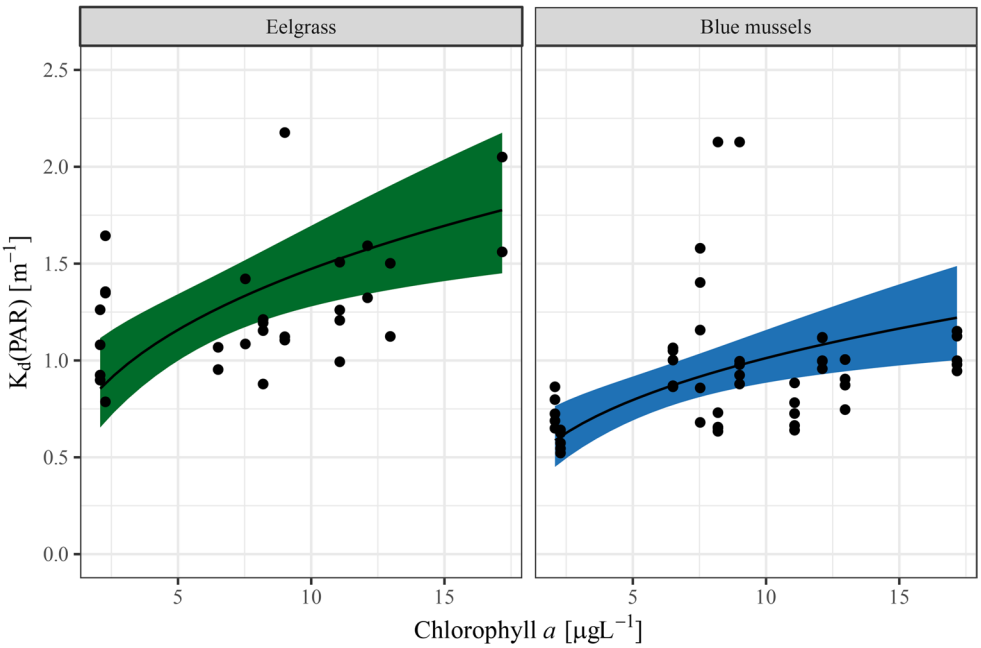


Fig. 6 Predictions of Kd(PAR) from the state-space model with fixed effects of habitat and chlorophyll a. Predictions were done on the scale of log(Kd(PAR)) with std. errs. estimated by RTMB to produce 95% CI on the log-scale and back-transformed to the real scale

velocity produced 1.3 delta AICc; omitting habitat produced 14.6 delta AICc; omitting chlorophyll *a* produced 78.5 delta AICc; omitting velocity and habitat produced 16 delta AICc. In this context, more than 14 delta AICc means that an effect has strong statistical support, while other smaller changes such as the 1.3 delta AICc for current velocity would indicate limited support (Murtaugh, 2014). An AICc table of all submodels is presented in supplementary materials. As current velocity improved the model fit to a minor degree, results are presented from the model without velocity (Fig. 6). Habitat and chlorophyll *a* were found to be the strongest temporal drivers of light attenuation.

Discussion

Blue Mussels Regulate Light Conditions Above Mussel Beds

Blue mussel beds were associated with consistently lower light attenuation than adjacent eelgrass meadows and mixed habitats, indicating that mussel filtration is a likely driver of improved near-bed light conditions in this shallow estuarine system. Across habitats, K_d(PAR) was lowest above blue mussel beds and highest above eelgrass meadows (Fig. 4), indicating a clear gradient in water clarity linked to habitat type. This pattern is consistent with the ability of suspension-feeding bivalves to reduce concentrations of suspended particles and phytoplankton, thereby increasing light penetration in the water column.

Our results are in line with previous studies from Limfjorden and other coastal systems showing reduced particle concentrations and enhanced water clarity above mussel beds (Petersen et al., 1997; Dolmer, 2000; Saurel et al., 2013). Blue mussels are known to improve light conditions mainly through water filtration (Riisgaard et al., 2004; Bos & van Katwijk, 2007; Wall et al., 2008; Gagnon et al., 2021). Mature beds of blue mussels can filter up to 170 m^3 m^{-2} d^{-1} under ideal conditions (Saurel et al., 2013), which allows for a substantial impact on suspended material and therefore the light conditions (Dolmer, 2000; Riisgaard et al., 2004; Nielsen & Vismann, 2014; Gagnon et al., 2021).

This is further supported by mesocosm experiments showing enhanced light availability in the water column from mussel filtration (Wall et al., 2008). Together, these results support the interpretation that the lower K_d(PAR) observed over mussel beds reflects active filtration rather than differences in background environmental conditions.

In shallow coastal systems, both suspended organic and inorganic particles can strongly influence light attenuation over the entire water column (Markager, 2004; Canal-Vergés et al., 2010; Paladini de Mendoza et al., 2018; Wen et al., 2018). Sediment resuspension is typically affected by water current velocity (Olesen, 1996). However, resuspension was unlikely to be a major driver of the observed differences in K_d(PAR) in Lovns Broad due to the low current velocity range observed and therefore limited resuspension (Canal-Vergés et al., 2010). The state-space models showed very little influence of current velocity on the temporal variation in K_d(PAR) compared to chlorophyll *a*, supporting that current induced resuspension did not impact light conditions. Current velocities during the study period were generally low and rarely exceeded reported thresholds for sediment resuspension (Canal-Vergés et al., 2010). Due to shallow depths and ADCP resolution limitations, our velocity data do not capture wave-orbital velocities near the bed, so wave-driven resuspension is not represented. Wind waves likely caused intermittent resuspension events, though these events were not frequently observed and did not persist for durations longer than a day. Similar conclusions have also previously been drawn for the Limfjorden, where relatively weak current regimes could not alone explain extensive turbulent mixing and particle resuspension (Wiles et al., 2006).

Taken together, these findings indicate that blue mussels act as local regulators of water clarity in Lovns Broad, primarily through their filtration rather than through reducing the strength and frequency of resuspension events. By reducing light attenuation above the mussel beds, mussels enhance light availability and can improve light conditions in adjacent habitats under favorable hydrodynamic conditions.

Hydrodynamic Connectivity Determines Whether Mussel Filtration Benefit Adjacent Eelgrass

The influence of blue mussel filtration on light conditions in adjacent habitats depended strongly on hydrodynamic connectivity between mussel beds and eelgrass meadows.

We found a clear difference in light attenuation in eelgrass beds depending on the current direction from either mussel-to-eelgrass or eelgrass-to-mussel (Table 1). When currents flowed from eelgrass toward blue mussel beds, light attenuation was substantially higher than over the mussels, whereas this difference was reduced when currents flowed from blue mussel beds toward eelgrass. The smaller difference in K_d(PAR) under mussel-to-eelgrass flow conditions indicates that water filtered by mussels reached downstream eelgrass meadows, improving light conditions relative to those upstream.

These findings provide in situ evidence for mussels' effect on light conditions are not confined to the mussel bed but can extend beyond and downstream of the mussel bed into adjacent habitats when the hydrodynamic conditions allow. These results are in line with Saurel et al. (2013), who demonstrated that mussel filtration can cause near-bed depletion extending beyond the physical edge of the mussel bed, with potential implications for the light conditions in adjacent waters. This supports the interpretation that directional flow enables mussels to influence water clarity at spatial scales relevant to eelgrass meadows.

However, hydrodynamics simultaneously constrains both the spatial reach of filtration effects and the stability of mussel beds themselves. Strong currents and turbulence can negatively affect mussel beds by increasing dislodgement, reducing bed stability, and limiting habitat persistence, thereby diminishing their overall ecological contribution (Bos & van Katwijk, 2007; Gagnon et al., 2021; Pajusalu et al., 2023). Conversely, a study from the Limfjorden suggests that effects of mussel filtration can be vertically restricted in low energy systems, as turbulent mixing over mussel beds does not extend substantially into the water column (Wiles et al., 2006). Together, these constraints define the hydrodynamic conditions under which mussel filtration can influence adjacent habitats and generate facilitative interactions with eelgrass.

Could Blue Mussel Beds Facilitate Improved Eelgrass Growth in Lovns Broad?

Light is a necessary habitat requirement for eelgrass and often the limiting factor for growth (Krause-Jensen et al., 2011). Our results demonstrate that blue mussel filtration can reduce light attenuation in downstream waters, indicating a clear potential to enhance light conditions for adjacent eelgrass meadows under favorable hydrodynamic conditions. Rather than demonstrating enhanced eelgrass growth directly, these findings identify a mechanistic pathway through which mussels may influence eelgrass growth in natural systems. This extends mesocosm-based evidence of mussel-facilitated eelgrass growth (Wall et al., 2008) to natural field settings by demonstrating the underlying light-related mechanism.

To assess whether filtration by blue mussels sufficiently improves light conditions for downstream eelgrass growth, the following factors should be evaluated. The growth of eelgrass is largely limited by light availability, although specific light requirements vary with environmental conditions.

Eelgrass generally has high light demands. Lee et al. (2007) report an average photosynthetic saturation around ~450 µmol m^{-2} s^{-1} and a minimum light requirement near ~85 µmol m^{-2} s^{-1}. In Danish estuaries, in-situ estimates of ecological compensation irradiance (ECI), the daily light dose required to maintain net shoot production, range from ~2.6 to 9.8 E m^{-2} d^{-1} (corresponding to 30–113 µmol m^{-2} s^{-1} as a daily mean), with higher values associated with eutrophication-related stress (Banke et al., 2025). At our northern site, daily mean irradiance at ~1 m depth in the eelgrass meadow was ~200 µmol m^{-2} s^{-1} (PAR), exceeding reported minimum and compensation requirements. This indicates that increasing light availability would likely benefit the eelgrass meadows and promote growth.

One of the largest constraints in this system is that filtered water must be transported to eelgrass meadows for a duration sufficient to affect growth. Based on the data from the northern site, the water current direction is rarely oriented in the desired direction and when it is, it is only in short time spans, i.e. >1 h after accounting for the time required for water to flow between habitats (Fig. 3a). This indicates that the effect of mussel filtration on eelgrass growth in this environment is likely restricted. This hydrodynamic limitation likely restricts the strength of facilitative effects on eelgrass growth at this site despite measurable improvements in light conditions.

In addition to hydrodynamic constraints, biogeochemical feedback may counteract the positive effects of improved light availability by facilitating other organisms. Blue mussels excrete dissolved inorganic nutrients that can stimulate epiphyte growth on eelgrass leaves, which has been shown to reduce eelgrass growth in both laboratory setting (Vinther & Holmer, 2008) and in a field study in Flensborg Fjord, Denmark (Vinther et al., 2008). Epiphyte overgrowth may reduce eelgrass productivity by inhibiting photosynthesis, with studies showing up to a 49% decline in photosynthetic efficiency (Drake et al., 2003; Noisette et al., 2022). In contrast, Ruesink (2016) demonstrated that reduced epiphyte load on eelgrass leaves does not necessarily accelerate growth, indicating that photosynthetic efficiency is not always directly linked to growth. Although epiphyte abundance was not quantified in the present study, this mechanism represents a plausible counteracting process that may offset benefits of improved light availability at the eelgrass leaves. Furthermore, dense beds of blue mussels can inhibit eelgrass growth through spatial competition (Allen & Williams, 2003). In contrast, eelgrass may benefit from co-existence, as mussels can reduce hydrodynamic exposure and increase survival of eelgrass shoots (Bos & van Katwijk, 2007).

It is also important to note that this study covered only a single growing season. Longer-term interactions, including gradual spatial competition or shifts in community structure, may therefore not be fully captured here. This temporal limitation should be considered when interpreting the results, particularly in the context of potential co-restoration or co-location of eelgrass and mussels. In the northern site, neither spatial competition, fertilization of the porewater, nor hydrodynamic release were considered crucial factors for eelgrass growth due to the segregation of habitats (Fig. 1c).

Overall, our findings indicate that blue mussels can facilitate improved light conditions for eelgrass, but that the ecological significance of this facilitation depends on spatial configuration and hydrodynamic connectivity.

Conclusion

We investigated facilitative effects between eelgrass and blue mussels, focusing on the mechanistic link between mussel filtration and light availability. Our results demonstrate that blue mussel beds reduce the light attenuation of photosynthetically active radiation, K_d(PAR), by removing phytoplankton from the water column, resulting in improved water clarity in mussel beds compared to eelgrass meadows. This filtration-driven improvement in water clarity can enhance light conditions for eelgrass located downstream of mussel beds, however, the magnitude of this facilitative effect is strongly constrained by hydrodynamic connectivity. The temporal coupling between mussel filtration and eelgrass exposure to improved light was restricted in this study area and consequently the effects on eelgrass growth were likely limited. Seasonal variation in light attenuation was primarily driven by changes in chlorophyll a rather than sediment resuspension, highlighting phytoplankton dynamics as the dominant control on underwater light climate in this system. Together, these findings indicate that mussels can improve light conditions for eelgrass when hydrodynamics are optimal.

From a management and restoration perspective, our results suggest that co-occurrence of mussels and eelgrass can enhance habitat suitability for eelgrass, but only in systems where hydrodynamic regimes allow sustained downstream transfer of filtered water. Restoration strategies that consider current direction and seasonal phytoplankton dynamics are therefore more likely to harness positive interactions and promote successful eelgrass recovery.

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Author Contributions Emil Hoffmann Bohr led the data analysis, interpretation and writing of the manuscript. Karen Timmermann, Tobias Kuhlmann Andersen and Daniel Taylor conceptualized and conceived the ideas and designed methodology; Daniel Taylor collected the data; Line Hermannsen pre-processed data and assisted with initial analysis and interpretation; Aris Thomasberger performed UAV surveys and habitat classifications; Mollie Elizabeth Brooks performed the statistics. Karen Timmermann was responsible for funding acquisition and project management. All authors contributed critically to the drafts, review and editing, and gave final approval for publication.

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Data Availability Field data and R code to reproduce the associated state-space models are available in a public repository on Figshare at https://doi.org/10.11583/DTU.31346785.

Declarations

Ethical Approval This article does not contain any studies with human participants or endangered animals.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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