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ORIGINAL PAPER

Can artificial magnetic fields alter the functional role of the blue mussel, *Mytilus edulis*?

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Abstract

Along European coasts, the rapid expansion of marine renewable energy devices and their buried power cables, raises major societal concerns regarding the potential effects of their magnetic field emissions (MFs) on marine species and ecosystem functioning. MFs occur at a local spatial scale, which makes sessile species the primary target of chronic and high-intensity exposures. Some of them, as ecosystem engineers, have critical functions in coastal habitats whose behavioral alteration may drive profound consequences at the ecosystem level. In this context, the present experimental study explored the effects of short exposure to direct current MFs, on the feeding behavior of a widespread ecosystem engineer, the blue mussel (*Mytilus edulis*). A repeated measure design was carried out with adult mussels successively exposed to control treatment (ambient magnetic field of 47 µT) and artificial MF treatment (direct current of 300 µT produced by Helmholtz coils), as measured around power cables. The filtration activity was assessed through valve gap monitoring using an automated image analysis system. The clearance rate was estimated simultaneously by measuring the decrease in algal concentration using flow cytometry. Our findings revealed that mussels placed in MF treatment did not exhibit observable differences in valve activity and filtration rate, thus suggesting that, at such an intensity, artificial MFs do not significantly impair their feeding behavior. However, additional research is required to investigate the sensitivity of other life stages, the effects of mid to long-term exposure to alternative and direct current fields and to test various MF intensities.

Keywords Magnetic fields · Submarine power cables · Ecosystem engineers · Coastal environments · Filter-feeders · *Mytilus edulis*

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Introduction

The adoption of renewable energy has become a priority for several developing countries in recent decades (Sen and Ganguly 2017). After a first phase of on-land projects, the development of the offshore renewable energy sector (i.e. wind, currents, waves) is currently prevailing and is generally considered a promising option to meet global energy demands (Gill 2005; Rinaldi 2020; Soares-Ramos et al. 2020). Moreover, the electrical interconnections between adjacent countries are intensifying to promote the production and widespread adoption of renewable energies (European commission 2019). Accordingly, the spread of submarine power cables to support electricity transfer in rich and sensitive coastal environments is becoming a major concern, particularly regarding the introduction of artificial magnetic fields (MFs) (Petersen and Malm 2006; Taormina et al. 2018).

MFs are defined as spaces that both influence and are influenced by electrical particles flowing through a power cable. Their strength or magnetic induction, which is measured in microteslas (μT), is proportional to the current intensity and sharply declines with distance from the cable (Normandeau et al. 2011; Otremba et al. 2019; Albert et al. 2020). MFs can also be influenced by other power line characteristics such as the number of conductors, the distance between them, the internal arrangement of copper wires (i.e. twisting) and the type of current: alternating or direct (AC or DC) (Meißner et al. 2006; Worzyk 2009; CSA Ocean Sciences Inc. and Exponent 2019). For example, DC cables produce static MFs that modify the ambient geomagnetic field (Otremba et al. 2019), whereas AC cables emit independent 50–60 Hz fields that vary over time (Kavet et al. 2016). Long-distance electricity transfer (> 50 km) is mainly achieved with high voltage direct current (HVDC) technology (Wei et al. 2017), whereas AC cables are preferred for shorter distances and often have lower transmission capacities (e.g. offshore wind farms) (Meißner et al. 2006).

Several marine species orient and navigate over short- or long-range migrations (e.g. for feeding, spawning, or reproduction), using the Earth's magnetic field (Wiltschko 1995; Walker et al. 2003; Vacha 2017). In the literature, such sensory modality is referred to as magneto-reception, magneto-sensitivity or magneto-sensation (Wiltschko 1995; Gill et al. 2014; Putman et al. 2022). By causing local geomagnetic field alterations, artificial MFs may thus impair the capacity of species to geolocate (Fischer and Slater 2010; Copping et al. 2016). Moreover, artificial MFs can be detrimental for biological structures, as for instance, they can delay embryonic development and increase the proportion of abnormalities in sea urchins and fish (e.g. Zimmerman et al. 1990; Levin and Ernst 1997; Li et al. 2014; Fey et al. 2019a, b). They can also magnify genotoxic and cytotoxic effects in polychaetes and bivalve mollusks (Stankevičiūtė et al. 2019). However, artificial MFs seem not to constitute an immediate threat to the survival of adult stages (Bochert and Zettler 2006; Jakubowska et al. 2019).

Current knowledge on the potential effects of artificial MFs remains highly inconclusive and heterogeneous across taxonomic groups (Petersen and Malm 2006). Particularly, invertebrates are largely under-represented in impact studies and data regarding their magneto-sensitivity is severely lacking (Isaacman and Lee 2009; Emma 2016; Albert et al. 2020). Yet, the likelihood of encountering MFs is highly dependent on the lifestyle of a given species, which in turn determines the duration and intensity of its exposure. Given that power cables are typically buried in the sediment (0.3 to 3 m depth), benthic, sessile and endogenous organisms such as bivalves, echinoderms, worms, and decapods would experience the highest values of magnetic induction, as opposed to pelagic species (Michel et al. 2007). For example, based on theoretical calculations, a 1000 A DC single-phase cable (15 cm diameter) would create 533 and 65 μT MFs at a 0.3 m and 3 m distance, respectively (the formula to calculate these estimates was obtained from Salinas et al. 2009).

So far, the effects of artificial MFs were mainly investigated in motile crustaceans. A few studies thus reported positive (Scott et al. 2018, 2021) or negative (Ernst and Lohmann 2018) taxis, changes in exploratory behaviors (Hutchison et al. 2020), disruption of orientation abilities (Tomanova and Vacha 2016), and alteration of physiological mechanisms (i.e. D-lactate, D-glucose and THC) controlling the circadian rhythm (Scott et al. 2018, 2021). Despite the risk of chronic exposure to artificial MFs, the sessile epifauna and sedentary endofauna have received far less attention. To our knowledge, only two species of sessile bivalves, the blue mussel (*Mytilus edulis*) and the Mediterranean mussel (*Mytilus galloprovincialis*), were used as biological models to highlight the effects of 50 Hz MFs on the immune system functionality (Ottaviani et al. 2002; Malagoli et al. 2003, 2004).

The filter-feeding bivalves are keystone species that control the benthic-pelagic coupling (Prins et al. 1997). These latter form a direct link between primary production and higher trophic levels by performing top-down control on phytoplankton biomass and composition through filtration (Cloern 1982; Stein et al. 1995; Bastviken et al. 1998). Moreover, they profoundly influence benthic remineralization processes and nutrient cycling through biodeposition (i.e. biogenic organic matter flux from the water column to the sediment surface) (Jansen et al. 2019). Up to now, the potential ecological consequences of MFs have not been evaluated on bivalve species at the organism, population

or community level. To address this issue, organism-level functional traits and behavior can be used as markers of physiological alteration due to their sensitivity to sublethal effects (Hasenbein et al. 2015). For instance, in bivalve filter-feeders, the feeding behavior is critical for the functioning of both individual energy metabolism and ecosystem functioning. This endpoint thus constitutes a biomarker with strong ecological value, whose impairment may lead to marked population-level consequences (Amiard-Triquet 2009; Hartmann et al. 2016). Mussel gaping/feeding behavior, typically occurs at a high and constant rate under an optimal range of algal concentrations (Riisgård et al. 2011). Conversely, at upper or lower critical thresholds, food availability leads to a reduction in valve gap and exhalant siphon area, as well as a retraction of mantle edges up to complete closure, which constitutes an adaptation to balance energetic gains and losses (Dolmer 2000; Riisgård et al. 2003; Maire et al. 2007). Bivalve gaping behavior is known to vary in response to several environmental parameters including temperature (Kittner and Riisgård 2005), salinity (Riisgård et al. 2013a, b), turbidity (Cranford 2019), flow velocity (Wildish and Miyares 1990), and food quality and quantity (Newell et al. 2001; Saurel et al. 2007). Moreover, valve gaping patterns, including valve-closure, are linked to the metabolic state of the mussel and can be used as bio-indicators of environmental stress (Hartmann et al. 2016; Redmond et al. 2017).

This study focuses on the blue mussel *Mytilus edulis* (Linnaeus, 1758), a widely distributed ecosystem engineer species that plays a central role in the functioning of coastal habitats (Commito et al. 2008). *M. edulis* is a gregarious intertidal to shallow subtidal organism that occurs in high population densities, forms large aggregated structures (Christensen et al. 2015) and dominates the French mussel farm production (Agreste 2019). In particular, it is a major colonizer of anthropogenic hard substrates of offshore buildings (Krone et al. 2013), such as wave power buoys and the foundations of offshore infrastructures (Joschko et al. 2008). Very few studies had evaluated the in situ biological colonization of submarine power cables (Carlier et al. 2019). However, using test equipment, Paschen et al. (2014) identified *M. edulis* colonies both on laid and free-flow cables located up to 10–12 m depths. Overall, mussel settlement is expected to be highly plausible over cables (or their protective structures) located in the intertidal and subtidal zones or over the cable sections located in open water.

Therefore, our study aimed to investigate the potential effects of DC MFs on the filtration activity of *M. edulis*, which may indirectly impair its ecosystem engineering role. To assess potential temporal changes, valve gap was measured over 6 h following a single algal addition using an automated image acquisition and analysis system (Maire et al. 2007). Short-term exposure to MFs was evaluated because mussels are known to instantly adjust their filtration behavior in response to external stimuli. Algal concentrations were also determined via flow cytometry to quantify filtration rates. The same individuals were tested under control (ambient magnetic field, 47 µT) and MF (homogeneous 300 µT) treatments.

Materials and methods

Magnetic field exposure device

Artificial MFs were produced using two squared Helmholtz coils (1.5 m × 1.5 m), each composed of 200 copper wire turns (2.5 mm^2 section) sealed inside a Plexiglas hollow frame. Both coils were placed vertically on Plexiglas racks, spaced 1 m apart, and connected with a branch circuit to a DC power supply (14.8 V; 4.6 A). This system, which will hereinafter be referred to as "Magnotron", produced a uniform 300 µT magnetic field within a tank equidistant from both coils (Fig. 1). Such value is the estimated magnetic induction at 0.6 m from a DC single-phase cable (15 cm diameter, 1000 A) (Salinas et al. 2009). The tank was used as a buffer to maintain a constant temperature inside two smaller experimental glass tanks filled with 10 L filtered still seawater (35 × 20 × 25 cm) (Fig. 1). The geomagnetic field inside the experimental tanks was measured at approximately 47 µT when the coils were turned off.

The Magnotron system functions in much the same way as other similar devices created by other research teams (e.g. Scott et al. 2018; Jakubowska et al. 2019), with the added benefit of being mobile and specifically designed for regular use across various experimental setups. Moreover, all electrical parameters (voltage, electric intensity, on/off switching, and coil temperature) can be monitored in real time, recorded, and programmed using a purpose-built software developed by MAPPEM Geophysics© (http://www.mappem-geophysics.com/). Magnetic induction is measured every 10 s by a magnetometer (Mag690 Three-axis, Bartington Instruments®) and maintained at a single intensity by an automatic control loop that continuously adjusts the electric intensity.

Mussel sampling and maintenance

Field sampling was conducted in February 2021 in the Bay of Brest (France, North-East Atlantic Ocean, 48°23′32.5"N–°25′59.3"W). Approximately 60 mussels (30–50 mm) were hand-collected from a natural bed located on floating docks. After removing epibionts through gentle brushing, individuals were kept in large tanks (60 × 50 × 40 cm; water depth: 30 cm) for a 9-day period, away from the Magnotron system and the emission of artificial MFs. The acclimation tanks were connected to

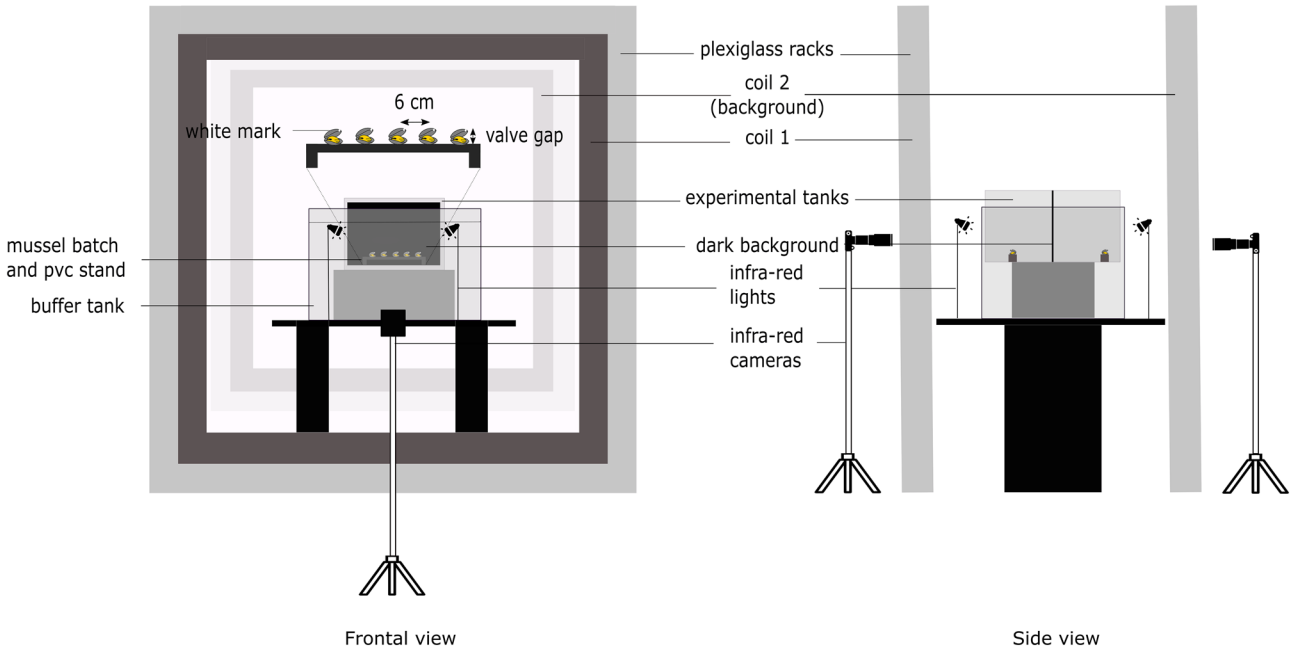

Fig. 1 Magnetic field exposure device: the Magnotron, with side and frontal views

a semi-closed water recirculating system with a 45% hourly renewal rate (84 L h^{-1} flux). The inflow was stopped for 3 h each day when bivalves were fed with an *Isochrysis galbana* monospecific culture (concentration of 3000 cells mL^{-1}). The water was directly pumped from the Bay of Brest and maintained at a natural temperature (approximately 12.6 °C) using a water chiller. The outflow of the tanks was filtered with a mechanical polyethylene filter followed by Biogrog® biological filtering and UV-radiation, before recirculation. Each tank was provided with an air pump to maintain air saturation levels > 98% (oxygen concentration > 8.7 mg L^{-1}). The pH and salinity were maintained at approximately 7.9 and 32.7 PSU, respectively, and other parameters were maintained below threshold values (NH_4^+ < 0.1 mg L^{-1}; NH_3 < 0.01 mg L^{-1}; NO_2 < 0.05 mg L^{-1}; NO_3 < 10 mg L^{-1}). To avoid a potential alteration of their filter-feeding activity caused by artificial light (Robson et al. 2010; Comeau et al. 2018), mussels were kept in total darkness during both the acclimation period and the experiments.

Experimental procedure

Twenty-four hours before, each experimental procedure 10 mussels were randomly collected and glued on two PVC stands using cyanoacrylate cement in groups of 5 at 6 cm intervals, and thus formed two mussel batches. A small white paint mark was then made on the margin of the free valve of each mussel (Fig. 1). To account for the high inter-individual variability of filtering activity in mussels, behavioral measurements were carried out through a repeated-measure design. For each set of experiment, two batches (5 mussels in each) were sequentially tested under control (CT treatment, 47 µT) on day 1 and magnetic field treatment (MF treatment, 300 µT) on day 2.

Before each treatment, the two mussel batches were starved overnight in two distinct 10 L tanks (i.e. 35 × 20 × 25 cm) filled with filtered (1 µm) seawater. On day 1, one hour before testing, both batches were transferred to the Magnotron's experimental tanks (Fig. 1). The coils were switched off during CT treatment. In CT or MF treatment, clearance rates and valve activity were then measured for 6 h (i.e. 21 600 s), at the batch (10 L, $n = 5$) and individual level, respectively, following the addition of an initial algal concentration of approximately 3000 cells mL^{-1} (*I. galbana)* (more details will be provided in the next section). Once the CT treatment ended, mussels were transferred back into the starvation tanks. On day 2, for the MF treatment, the same mussel batches were submitted to a 300 µT MF, that was initiated prior to their transfer and the same set of measurements was collected. Apart from the 300 µT MF, all other experimental conditions were strictly similar. In total, filter feeding activity was monitored in six batches of five mussels, i.e. a total of 30 individuals.

Monitoring of valve activity

The distance between the two valves was monitored using an automated image acquisition system consisting of an infrared camera (uEye® camera fitted with a 25 mm Fujinon®

objective lens) connected to a laptop computer driven by the Obvious MicroLum software developed at the EPOC Laboratory, University of Bordeaux (Romero-Ramirez et al. 2016). The video sensor was located 110 cm in front of the mussels and infrared lights maximized the contrast between the white mark and the mussel shell. As recommended by Maire et al. (2007), gray-scale images were acquired every 10 s and gathered into an AVI file (5 frames s^{-1}). The AVI explore software was then used to measure the valve gap through the detection of the white mark successive positions, based on pixel color. For each image, the valve gap was expressed as the distance in pixels between *y*-coordinates (y_n) of the white mark barycenter (i.e. center of mass) and a reference point (y_0), corresponding to complete closure. Valve gap data were converted into mm and then into angles Θ (expressed in degrees) using the following equation from (Wilson et al. 2005), where W is the valve gap (mm) and L is the maximum shell length (mm).

$$\theta = 2\arcsin\left(\frac{0.5W}{L}\right) \times 100 \quad (1)$$

Measurement of filtration rates

Filtration rates were quantified using the clearance method (Coughlan 1969) defined as the volume of water cleared of algal cells per unit of time. *Isochrysis galbana* cells (4.5 µm diameter) have an optimal retention efficiency in *Mytilus edulis*, as their size is above the 100% retention efficiency threshold, and therefore the clearance rate is equal to the filtration rate (Møhlenberg and Riisgård 1978). The filtration rate of *M. edulis* remains high and constant at concentrations ranging from 2000 to 6000 cells mL^{-1} (Riisgård 1991), which is consistent with the phytoplankton winter concentrations observed in the Bay of Brest (Delmas et al. 1983; Hafsaoui et al. 1985). Accordingly, all experiments were performed at an initial algal concentration of approximately 3000 cells mL^{-1} (corresponding to 9.32 10^{-5} mg dry weight (DW) mL^{-1} and 2.98 10^{-5} mg C mL^{-1}, from Maire et al. 2007). During the experiments, water was continuously aerated with air bubbling to maintain a homogeneous concentration of suspended algal cells. Water samples (0.5 mL in triplicates) were collected at the center of each tank 10 min after algal addition and then every 20 min. The samples were kept in cryotubes filled with 10 µL glutaraldehyde solution, for cell fixation, and stored at −80 °C.

Cell counting (cell mL^{-1}) was performed using a Guava® easyCyte™ 5HT flow cytometer (LUMINEX, 12212 Technology Blvd, Austin, Texas USA). The system was equipped with a 488-nm argon laser (50 mW), forward (FSC) and side scatter (SSC) detectors for relative cell size and complexity, respectively, and three fluorescence detectors: Green-B (525/30 nm), Yellow-B (583/26 nm) and Red-B (695/50 nm). Further, the system was also equipped with a direct, absolute cell count system. Samples were distributed in 96-well micro-plates and analyzed in the flow cytometer for 90 s at a high flow rate (1.18 µL s^{-1}). Phytoplankton cells were selected according to their relative size and/or complexity (FSC/SSC) and their red fluorescence after exciting the chlorophyll pigments with a blue laser. Gating of cells of interest was performed using the Guava SOFT 4.0 software.

Water samples without mussels were also collected to measure algal loss due to sedimentation. In all experiments, clearance rates were calculated at the batch level, as previously described (Maire et al. 2007):

$$\text{CR } or\ F = V \times b \quad (2)$$

where CR is the clearance rate (L h^{-1}) and is equivalent to the filtration rate F; V is the water volume (10 L) and b is the slope of the linear regression line representing the gradual reduction in algae concentration ($R^2 > 0.72$). Algal sedimentation was highly negligible (± 100 cells). At the end of each experiment, individual measurements of maximal shell length (L; in cm) and flesh dry weight (DW; in mg) (24 h, 77 °C) were performed to calculate the condition index (CI) (Supplementary Material A):

$$\text{CI} = \frac{\text{DW}}{L^3} \quad (3)$$

Statistical analyses

Before conducting the analysis, valve angles were converted to percentages of the maximum value recorded over the experiment and distributed into 10 ranges in steps of 10%. Using principal component analysis (PCA), ranges (%) were condensed into higher grouping categories that were compared using the Kruskal–Wallis and Wilcoxon tests. PCA was based on a covariance matrix and principal components were chosen based on Kaiser's criterion (Kaiser 1960) (Supplementary Material B and C). Feeding responses occurred in two periods, P1 and P2. P1 period started with algal addition ($T = 0$) and was characterized by an increase in valve angle, which then reached maximal values. During the P2 period, valve angle was generally high and rather constant but then declined gradually in response to low algal concentrations (< 500 cell mL^{-1}). Mussel filtration activity was described by a set of 7 response variables: P1 duration (h), batch filtration rate (L h^{-1} ind^{-1}), mean valve angle over P2, and average duration (s) spent in the four valve angle categories derived from PCA ('low,' 'average,' 'high,' and 'maximum'). The relationships between the aforementioned response variables and the treatment (CT or MF) was assessed using linear mixed effect models (LMM), as described by (Brown 2021). Magnetic treatment and one

of the seven response variables were entered as fixed effects and batch number was nested within the treatment variable for the random structure. Models were selected based on the Akaike information criterion (AIC) and maximum likelihood estimations. The effect of MF was investigated by likelihood-ratio tests and PCA and LMM were respectively conducted using the 'nlme' (Pinheiro and Bates 2000), and 'ez' packages in R version 4.0.2 (R Core Team 2021). Assumptions of residual normality and homoscedasticity were verified by plotting the residuals versus the fitted values. All statistical analyses were performed at a significance level of 5%.

Results

From the 30 tested individuals (6 batches × 5 mussels), 10 were excluded from valve angle analysis due to the absence of filter-feeding activity in at least one of the two treatments. These mussels remained either closed during both the CT and MF treatments ($n=5$) or had no distinct P1 and P2 periods ($n=2$ in CT and $n=3$ in MF). In total, the valve activity was thus monitored in 20 mussels (the biometrical characteristics of these organisms are provided in Supplementary Material A). All individuals from the two treatments quickly opened between 14 and 97% of the valve angle after algal addition ($T=10$ min), with a mean (± standard error) of 60.9% ± 4.3% and 60.2% ± 4.0% in the CT and MF treatment, respectively. The filtration rate was calculated at the batch level for comparisons between treatments, and was estimated a posteriori at the individual level, excluding mussels that remained totally closed during the duration of the experiments ($n=22$ and $n=23$ in CT and MF treatments, respectively).

P1 duration, P2 mean valve angle, and filtration rates

The duration of P1 (i.e. the initial period of valve gap increase in response to algal addition) varied from 0.44 to 2.90 h, with a mean (± standard error) of 1.15 ± 0.14 h in the CT treatment and 0.93 ± 0.09 h in the MF treatment. The mean valve angle during the P2 period (i.e. the period of high and constant valve angle) was 11.52 ± 0.74° and 9.77 ± 0.64° in the CT and MF treatments, respectively (Table 1). Figure 2 illustrates a typical valve angle temporal variation as a function of algal concentration. During the experiment, the average batch filtration rates were 8.06 ± 1.66 L h^{-1} in the CT treatment and 7.54 ± 1.20 L h^{-1} in the MF treatment (Table 2 and Fig. 3). None of these response variables varied significantly as a function of

Table 1 Experimental response variables describing the valve activity across mussel (*Mytilus edulis*) batches as a function of magnetic treatment (CT at 47 µT and MF at 300 µT)

Batch	Temperature (°C)		Mean duration of P1 ± SD (s)		Mean valve angle over P2 ± SD (°)	
Treatment	CT	MF	CT	MF	CT	MF
1 $n=4$	13.0	13.1	4310 ± 3190	2215 ± 394	8.48 ± 3.22	9.50 ± 0.82
2 $n=2$	12.5	12.9	6690 ± 5303	3770 ± 651	11.52 ± 0.67	7.85 ± 1.29
3 $n=3$	13.2	15.1	3963 ± 2550	5630 ± 485	14.80 ± 1.46	11.37 ± 1.94
4 $n=4$	13.2	15.2	3322 ± 895	2700 ± 645	10.58 ± 1.92	6.44 ± 2.57
5 $n=3$	12.9	12.8	3997 ± 1451	1643 ± 67	14.21 ± 2.42	10.01 ± 2.63
6 $n=4$	15.0	17.4	3718 ± 1095	4420 ± 878	11.02 ± 4.48	12.94 ± 1.82
Mean ± SE			4133 ± 503	3335 ± 329	11.52 ± 0.74	9.77 ± 0.64
P value					0.346	0.094

n is the number of mussels that displayed a filtering activity and had discernible P1 and P2 periods. *P* values were obtained from linear mixed-effect modelling (LMM) using likelihood ratio tests. SD, standard deviation; SE, standard error. The experimental lasted 6 h (21 600 s) in total

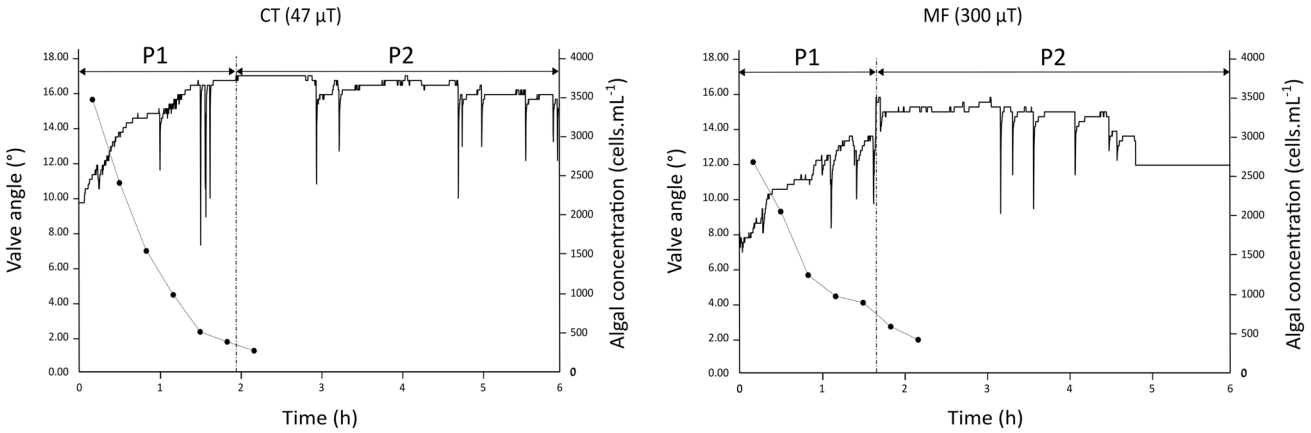

Fig. 2 Example of the temporal changes in valve angle of one *Mytilus edulis* individual (solid line, °) in relation with algal concentration (filled circles, cells mL^{-1}), across CT and MF treatments. Algae were added at $T=0$ and counted from $T=10$ min. The P1 period starts with algal addition and is characterized by an increase in valve angle up to maximal values. The P2 period is characterized by a high and constant valve angle that gradually declined with low algal concentrations. The limit between P1 and P2 is indicated by the dashed vertical line

magnetic treatment (P1 duration: L.ratio = 0.89, $p=0.346$; P2 valve angle: L.ratio = 2.81, $p=0.094$, filtration rate: L.ratio = 0.08, $p=0.782$).

Time spent in different valve angle categories

Using PCA, valve angle ranges were classified into four groups: 'low' (i.e. 0–10%; 10–20%), 'average' (i.e. 20–30%; 30–40%; 40–50%; 50–60%), 'high' (i.e. 60–70%; 80–90%) and 'maximal' (i.e. 90–100%) valve angles (Supplementary Material B and C). The percentage of time (%) spent across the different categories in both treatments is illustrated in Fig. 4. Irrespective of the treatments (CT vs MF), there was a significant difference in the time spent across the four valve angle categories (χ^2 (3) = 54.40, $p<0.01$, size effect = 0.33). Overall, the mussels spent 5% of the time at low aperture, 20% at average aperture, 45% at high aperture, and 32% at maximum valve aperture. Particularly, pair-wise comparisons demonstrated that the mussels spent significantly less time at low valve aperture relative to all other categories (Wilcoxon test: $p<0.01$ in all comparisons), and the time spent in the average category was significantly below that spent in the high category (W. test: $p<0.01$). Nevertheless, the MF did not impact the time spent in neither the low (L.ratio = 0.91, $p=0.313$), average (L.ratio = 0.01, $p=0.900$), high (L.ratio = 0.22, $p=0.720$), nor maximal valve angle (L.ratio = 0.8, $p=0.420$).

Discussion

Despite the rapid development of offshore renewable energies and the subsequent expansion of submarine power cables, research on the effects of their emissions on marine fauna and especially sessile invertebrates, which are particularly exposed, is still very scarce. To our knowledge, this study is the first to investigate the effects of 300 µT DC magnetic fields on a key ecological function, the filtration activity of suspension-feeding bivalves. To detect potential behavioral changes caused by the MFs, one critical aspect of the experiments was to be sure that mussels displayed a natural feeding behavior that was not altered by the experimental conditions (e.g. light, algal concentration). To this end, similar and optimal conditions for filtration activity were provided to the mussels across the treatments. The initial cell concentration (3000 cells mL^{-1}) matched the natural seasonal algal concentration at the sampling site (Delmas et al. 1983) and was optimal for the expression of a natural feeding behavior in the blue mussel (Riisgard 1991). In addition, given that *M. edulis* tends to reduce its feeding behavior below 800–500 cells. mL^{-1} (see Fig. 2B in Riisgard et al. 2003), the addition of an initial moderate concentration allowed for the observation of both the increase of the filtration rate (i.e. immediately following algal cells addition) and the reduction of the filtering activity (caused by food limitation), within the experiment duration.

The present results demonstrated that a 300 µT DC magnetic field does not disturb the filter-feeding activity of the blue mussel neither in terms of valve activity nor filtration rate. In particular, there were no changes in the valve angle in relation with algal concentration and the filtration rate remained similar compared to the control treatment

Table 2 Parameters of clearance experiments obtained for mussel (*Mytilus edulis*) batches ($n = 5$) as a function of magnetic treatment (CT at 47 µT and MF at 300 µT): b = slope of the linear regression line (min^{-1}), R^2 = correlation coefficient, F_{batch} = filtration rate of the batch (L h^{-1}), α = number of mussels that remained opened during the entire duration of the experiment (6 h)

Batch	1		2		3		4		5		6	
Treatment	CT	MF	CT	MF	CT	MF	CT	MF	CT	MF	CT	MF
b	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.02	0.01
R^2	0.99	0.99	0.99	0.93	0.99	0.98	0.98	0.99	0.96	0.98	0.98	0.72
F_{batch}	7.56	8.64	3.00	11.40	13.20	9.00	8.40	7.80	4.20	5.40	12.00	3.00
A	4	4	2	3	4	4	4	5	4	3	4	4
$\frac{F_{batch}}{\alpha}$	1.89	2.16	1.50	3.80	3.30	2.25	2.10	1.56	1.05	1.80	3.00	0.75

F_{batch} was divided by α to estimate the average individual filtration rates (L h^{-1})

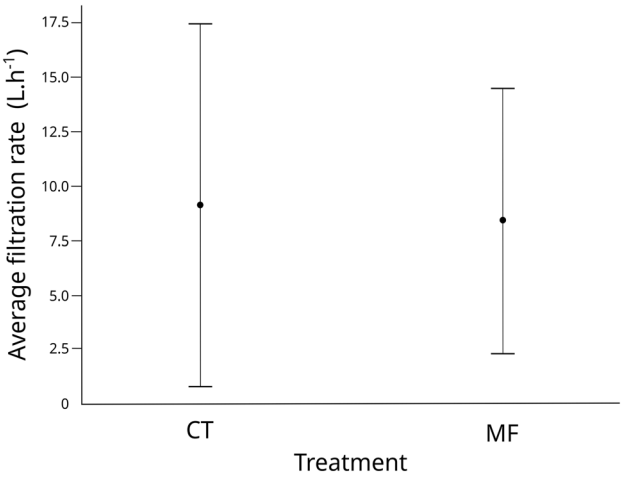

Fig. 3 Average filtration rates (L h^{-1}) of mussel batches (*Mytilus edulis*) (10 L, $n = 5$) during the CT (47 µT) and the DC (300 µT) treatments. Error bars represent 95% confidence interval of the mean. The same individuals were tested sequentially across the CT and then the MF treatment

(47 µT geomagnetic field). Therefore, individual filtration rates, standardized to DW (g), averaged (± standard error) 6.71 ± 1.04 L h^{-1} g DW^{-1} and 7.60 ± 1.73 L h^{-1} g DW^{-1} under the CT (47 µT) and MF treatment (DC 300 µT), respectively. These values were fully consistent with the range previously reported for this species in the literature (e.g. 5.39–8.08 L h^{-1} g DW^{-1}) (Riisgård et al. 2011). Our specimens had a mean condition index of 3.9 ± 1.0 mg cm^{-3}, which was at the lower end of the typical species range according to the seasonal maturation cycle (3.6–8.4 mg cm^{-3}, Bayne and Worrall 1980). Temporal changes in valve opening during the whole duration of the experiments were similar to those described in earlier studies (e.g. Dolmer 2000; Newell et al. 2001; Riisgård et al. 2003). Particularly, following algal addition, the valve angle of the mussels reached maximum values, on average, at 1.15 h in the CT treatment and 0.93 h in the MF treatment. By comparison, Riisgård et al. (2003) estimated the duration of this opening phase around 45 min in *M. edulis* and Maire et al. (2007) around 1.3 h in the Mediterranean mussel *M. galloprovincialis*. Afterward, bivalves typically maintain filtration rates at their maximal capacity with a constant valve gap until algal concentrations decrease below a critical threshold. Due to a moderate addition of food (3000 cells mL^{-1}) at the beginning of the experiment, the conditions became suboptimal for the mussel's filtration activity after about 1–2 h, which may explain lower values of filtration rates compared to previous studies (Riisgard et al. 2013a). As reported by Riisgård et al. (2003, 2013b), actively feeding bivalves rapidly reduced their filtration activity when the algal concentration decreased below 1000 cells mL^{-1}. Although the period (P2) of decreasing valve angle could not exceed the 6 h duration

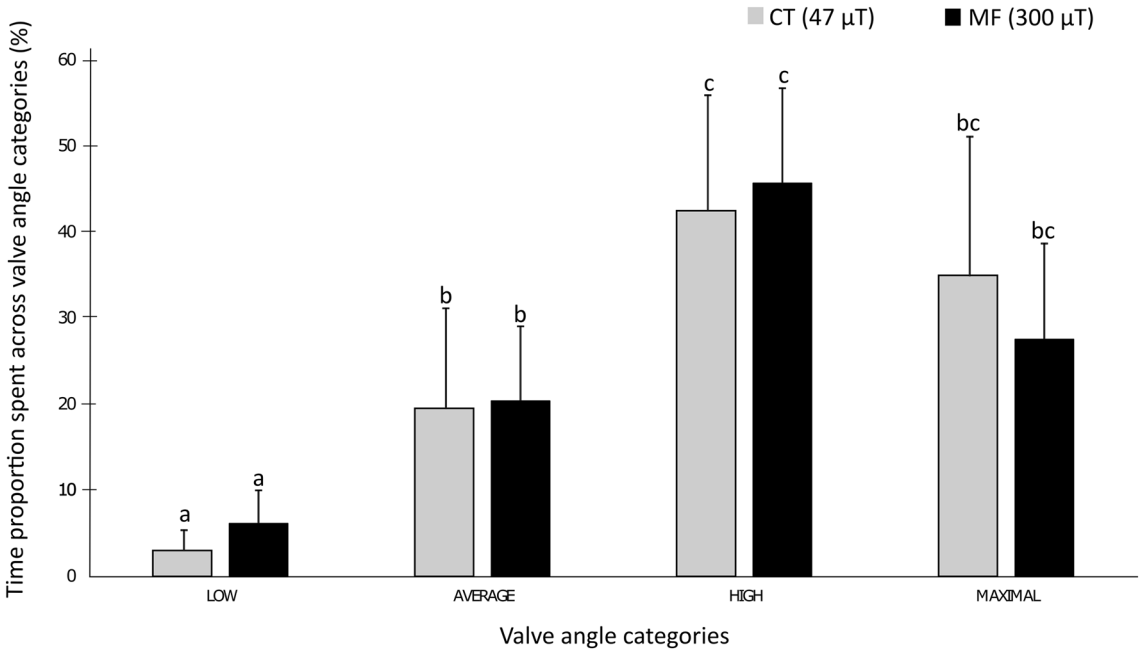

Fig. 4 Time proportion (%) spent by mussels (*Mytilus edulis*) across the four categories of valve angle opening: low (0–20%), average (20–60%), high (60–90%), and maximal (90–100%) in the CT and MF treatments. The same individuals were tested across both treatments. The histograms that do not share common letters are statistically different ($p < 0.01$)

of the experiments, only few mussels displayed complete closure of the valves, which can last up to 500 min in *M. edulis* (Riisgård et al. 2003). However, there were no significant differences between treatments in temporal changes of valve angle during this P2 period.

In the present study, one-third of the individuals were excluded from the analysis because they remained closed or did not exhibit typical filter-feeding signals. Such response patterns were analogous to the avoidance behavior, described as a stress response to chemicals, in which mussels keep their valves closed (Hartmann et al. 2016). Avoidance behavior is identified as a reliable sublethal indicator of mussel short-term disturbance. However, none of the closures were specific to the MF treatment and always occurred in both treatments. Additionally, some individuals displayed filtering activity in only one treatment but independently of CT or MF. Since the experimental sequence (CT before DC) was kept constant across all mussel batches, the absence of filtration may not be due to post-exposure effects. Therefore, we concluded that MF was not the cause of mussel long-term closing and, overall, that filtration activity of adult mussels was not significantly affected by MF short-term exposure. Behavioral differences observed both within and between treatments were likely attributable to the high natural inter-individual variability of acclimation to transfer, captivity, and other experimental conditions.

As previously acknowledged, data regarding the effects of artificial MFs on bivalves are severely lacking and behavioral measurements are still absent from the literature. In that respect, the present findings cannot be compared or discussed with a directly relevant literature. Nonetheless, some studies addressed the issue at the physiological scale in the blue mussel (*M. edulis*) and the Baltic clam (*Limecola balthica*) (Bochert and Zettler 2006; Stankevičiūtė et al. 2019). The authors reported that long-term exposure to strong MF intensities (mussel: 3.7 mT DC for 52 days; clam: 0.85–1.05 mT AC for 12 days) was neither a threat to the bivalves' survival nor to *M. edulis* reproductive status. Nevertheless, the immune system of the Mediterranean mussel (*M. galloprovincialis*) was altered after short-term MF exposure (300–1000 µT at 50 Hz AC, for 15–30 min). Further, the authors identified disruptions in the cellular processes and an increase in genotoxic and cytotoxic effects in the gill cells of the Baltic clam (Ottaviani et al. 2002; Malagoli et al. 2003, 2004; Stankevičiūtė et al. 2019). In marine species, apoptosis and DNA damage are common biomarkers of environmental stress (Falfushynska et al. 2021). Based on this broad-spectrum ecotoxicological approach, MFs may activate the physiological pathways commonly associated with organic contaminants in bivalves. Currently, the leading hypothesis is that MFs would trigger oxidative stress mechanisms (Mahmoudinasab et al. 2016). Further, 48-h experiments were also conducted in freshwater invertebrates (e.g. the snail *Elimia clavaeformis* and the clam *Corbicula fluminea)* and found no changes in the spatial distribution patterns relative to the location of a magnet (maximum of 36

mT DC) (Cada et al. 2011). Overall, the few results obtained so far suggest that artificial MFs cause alterations of the biological system that do not occur at organism-level life traits.

When facing environmental stressors, organisms maintain homeostasis through a suite of adaptive mechanisms at the molecular, biochemical, physiological, and behavioral scales (Goldstein and Kopin 2007). Changes in behavioral patterns may occur as part of a tertiary response level to stress that is modulated by the timing, intensity, persistence, and predictability of the stressor, as well as the genetic traits and conditions of the individual (Barton et al. 1987). Accordingly, in an experimental context, the choice of exposure duration is highly critical as it may interfere with the sensitivity of the behavior assessed (Amiard-Triquet 2009). Until now, neither work, including this one, has conclusively demonstrated that short-term continuous exposure to MFs induces behavioral changes in marine mollusks. This may suggest that tertiary stress responses occur over longer-term continuous exposures. In such case, given that MFs are predictable and of prolonged nature, the outcome might either be habituation with a decrease in response to MF stimuli (Dehaudt et al. 2019) or a maladaptive stress response with potential adverse effects on reproductive success (Suri and Vaidya 2015).

Research conducted on marine bivalves indicated that some effects of MFs would be transitory and that compensatory mechanisms would be implemented at the physiological scale. Studies in *M. galloprovincialis* indeed demonstrated that immune system alterations (delay in cell adhesion and shape changes) under 300 to 600 µT AC MFs were transitory and reversible (Ottaviani et al. 2002; Malagoli et al. 2003). The authors identified the activation of an alternative stress pathway involved in restoring homeostasis in exposed individuals. Remarkably, MFs have also been found to cause intensity-dependent effects, with no alterations at 200 µT, temporary damages from 300 to 600 µT, and permanent alterations above 600 µT up to 1000 µT. Hence, future dose–response investigations at all stress response levels and with realistic DC and AC MFs intensities are fundamental to assess the environmental impacts of power cables.

Furthermore, the effects of MFs on organisms must also be addressed in the context of their life history and habitat. This would effectively account for the concept of critical windows of exposure (or sensitive periods), over which the individual phenotypic plasticity is higher and largely shaped by environmental or intrinsic factors (Burggren and Mueller 2015). For instance, mussel reproductive metabolism is considered a major confounding factor in monitoring their biological responses (Farcy et al. 2013). As a result, the present work was purposely performed at the end of gonadal development to avoid vulnerable periods of the mussel life cycle. Nevertheless, organisms in poor physiological conditions, such as immediately after a spawning event, might be particularly vulnerable to MF-mediated stress (Berthelin et al. 2000). Similarly, other life stages (e.g. larval fixation stages) must also be considered, as they are generally more sensitive to abiotic factors and might be more responsive to MFs (Gosling 2003). For example, bivalves metamorphosis (pediveliger larvae) is a critical process whose success depends on a wide range of factors (e.g. temperature, food supply, suitable substrate availability, and other biological, physical, and chemical stimuli), which is also vulnerable to exogenous factors (Toupoint 2012). In spite of such context, data about bivalves larval stages are absent from the literature and are strongly needed.

Conclusion

This pioneering study demonstrated that short-term exposure to DC 300 µT magnetic fields had no observable effects on the filtration activity of *Mytilus edulis*. Feeding behavior has a strong ecological value and our findings provide seminal insights into the potential effects of MFs at the population level. However, additional work is needed to explore the interactions between the intensity and duration of MF exposure, as well as the effects of alternating current and other environmental factors on mussel behavior. Further, the effects of MFs on different life stages and vital functions of marine invertebrates must also be evaluated to determine their population-wide implications.

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Author contributions LA: conceptualization, methodology, validation, formal analysis, investigation, writing-original draft, writing-review and editing, visualization. OM: conceptualization, methodology, validation, writing-review and editing, supervision, resources. FO: conceptualization, methodology, writing-review and editing, supervision. CL: writing-review and editing, methodology, resources, investigation. AR-R: methodology, formal analysis, validation. AJ: conceptualization, methodology, writing-review and editing, supervision. LC: conceptualization, methodology, project administration, supervision, funding acquisition. SC: conceptualization, methodology, project administration, supervision, funding acquisition.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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

Ethics approval National guidelines for mussel collection have been followed.

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