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Research article

Density-dependent effects of parasitism on the activity of a benthic engineer species: potential impact on ecosystem functioning

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While parasitism is a common lifestyle on Earth, its importance for the functioning of marine ecosystems has been overlooked for a long time. In particular, parasites have significant potential to influence central ecological processes through their impacts on hosts that serve as ecosystem engineers. Using an ex situ experimental approach, we explored the effects of trematode parasites on the engineering bioturbation activity of a common and abundant bivalve along European Atlantic soft-bottom coastlines, the peppery furrow shell *Scrobicularia plana*, as well as knock-on effects for nutrient exchanges at the sediment–water interface (SWI). Trematodes negatively impacted the host's ability to transport sediment particles and solutes in a density-dependent way, with parasite burden explaining 22–31% of the inter-individual variability. This could be explained by parasitism impairing the bivalve physiological state and ability to burrow, as we observed a decrease in the condition index and the burrowing depth of the bivalves with an increase in the number of parasites they host. In contrast, the influence of *S. plana* on benthic biogeochemical fluxes did not vary significantly according to parasitic burden over a short time scale. Here, we focused on the effects of trematode parasites on the behaviour of *S. plana* alone, and thus excluded other macrofaunal organisms. We should next test whether trematodes modulate the structure and functioning of benthic communities dominated by *S. plana* to better understand and quantify the engineering role of parasites in soft-bottom coastal environments.

Keywords: benthic ecology, bioturbation, nutrient cycling, trait-mediated effects, trematode parasites

Introduction

Parasitism is one of the most ancient and common lifestyles on Earth, with 30–50% of all eukaryotes estimated to be parasitic (Windsor 1998, de Meeûs and Renaud 2002, Dobson et al. 2008, Poulin 2014). As widespread organisms, parasites are



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critical components of natural systems and important ecological forces for the functioning of both terrestrial and marine ecosystems (Hatcher et al. 2012, Preston et al. 2016). For instance, they can modulate ecological processes through changes in host mortality and/or reproduction rates (Pearre 1976, Lauckner 1987, Mouritsen and Jensen 1994, Desclaux et al. 2004) that directly control population demography (density-dependent effect) (Anderson 1978, Hochberg 1989, Hudson et al. 1998). Parasites also have sublethal effects on hosts and can modulate traits such as growth rates (Mouritsen and Jensen 1994, de Montaudouin et al. 2012), feeding rates (Anderson 1975, Hernandez and Sukhdeo 2008) or behaviour (Mouritsen and Poulin 2005, Dairain et al. 2020, Pascal et al. 2020). Both density-dependent and trait-mediated effects of parasites can lead to broader structural and functional consequences that extend beyond their direct effects on host populations. For instance, parasites can influence the outcome of interspecific interactions (Price et al. 1986, Lafferty 1999), and thus of community composition and structure (Minchella and Scott 1991, Mouritsen and Poulin 2002, Wood et al. 2007). Therefore, parasites can have indirect ecosystem-wide effects as they contribute to energetics, temporal dynamics and the stability of natural ecosystems (Hatcher et al. 2012, Preston et al. 2016).

Parasites that 1) are prevalent among organisms that possess unique functional traits and 2) have a substantial propensity to influence those traits are likely to noticeably influence ecosystem processes (Thomas et al. 1999, Preston et al. 2016, Dairain et al. 2019). In marine soft-bottom ecosystems, bioturbating organisms constitute a critical functional group of hosts for parasites (Dairain et al. 2019). The group comprises macro- and meiofaunal organisms living on the surface of or within the sediment matrix. Through their behaviours, these organisms induce intense sediment particle and porewater transport (Kristensen et al. 2012) with cascading effects on sediment geomorphology (Rhoads and Young 1970, Jones and Jago 1993), biogeochemistry (Aller 1982) and benthopelagic coupling (Lohrer et al. 2004, Le Hir et al. 2007). By inducing changes in the behaviour of their bioturbating hosts, parasites have the potential to influence central ecological processes in marine soft-bottom environments (Thomas et al. 1999, Mouritsen 2004, Mouritsen and Poulin 2005, 2010, Dairain et al. 2019). For instance, the trematode *Curtuteria australis* greatly influences the engineering role of its host, the New Zealand cockle *Austrovenus stutchburyi*. Cockles *A. stutchburyi* normally live buried in the first few centimetres below the sediment surface along sheltered shores of New Zealand. Heavily parasitized cockles show a reduced ability to burrow (Thomas and Poulin 1998) and lowered crawling activity at the sediment surface (Mouritsen and Poulin 2005). The bioturbation activity of the bivalve largely depends on its locomotory potential, and heavily parasitized organisms show a lower sediment reworking rate than non-parasitized conspecifics. The lower sediment disturbing effect of parasitized organisms results in changes in the structure of the benthic community, modifications of

the sediment characteristics and seabed elevation (Mouritsen 2004, Mouritsen and Poulin 2005, 2010).

Digenetic trematodes are a major group of parasites that infect bioturbators (Dairain et al. 2019). These helminths have complex life cycles. In the mollusc, that is the first intermediate host, trematodes occur as sporocysts (or sometimes rediae), and encyst as metacercariae in the mollusc, polychaete or crustacean, that is the second intermediate host (Rohde 2005 for details about the life cycle). Prevalence of trematodes (percent of infected hosts) in second intermediate host populations can reach 100% (Sousa 1991, Dairain et al. 2019), while the intensity of infection (number of parasites per host) can strongly vary between individuals, at both small and large spatial scales (de Montaudouin et al. 2009, Dairain et al. 2017). It is usually assumed that the metacercarial stage is relatively benign because metacercariae are asexual and grow little in their host (Lauckner 1980, 1983, Rohde 2005). Nonetheless, this general view has important exceptions, and a density-dependent negative effect of metacercariae has been detected in several host–parasite systems (Lafferty and Morris 1996, Mouritsen 2002, Fredensborg et al. 2004, Thielges 2006, O’Connell-Milne et al. 2016). For example, Lafferty and Morris (1996) found a strong positive relationship between conspicuous behaviours of the Pacific killifish *Fundulus parvipinnis* and infection intensity with metacercariae of *Euhaplorchis californiensis*. Similarly, Mouritsen (2002) demonstrated that the ability of cockles *A. stutchburyi* to contract their foot decreased as a function of infection intensity with *C. australis*, which could explain the impaired locomotor capacity of *A. stutchburyi* noticed by others, as the bivalve’s digging and crawling activities depend on its foot movements (Thomas and Poulin 1998, Thomas et al. 1998).

Many bioturbators are hosts for a myriad of parasites (Dairain et al. 2019), but thus far, fewer than ten studies have assessed the behavioural consequences of parasite infection on bioturbating hosts, including knock-on effects for ecosystem processes (Thomas et al. 1998, Mouritsen and Poulin 2005, Mouritsen and Haun 2008, Simão et al. 2010, Dairain et al. 2020, Pascal et al. 2020, Richard et al. 2021). Further research is thus necessary to better apprehend how interspecific interactions involving inconspicuous partners shape the functioning of marine soft-bottom ecosystems. We thus performed laboratory experiments involving the peppery furrow shell *Scrobicularia plana* and trematodes *Himasthla* spp. as a model host–parasite system to test whether trematodes can alter the behaviour of a second intermediate bioturbating host, and evaluated the consequences of potential behavioural changes for ecosystem functioning by measuring biogeochemical fluxes across the sediment–water interface (SWI). The peppery furrow shell is a large, facultative deposit-feeding bivalve (Hughes 1969, Riera et al. 1999) that is widespread and abundant in coastal soft-bottom environments along the east Atlantic, Mediterranean and Baltic Sea coastlines (Santos et al. 2011). The bivalve feeding and locomotory activities (valve clapping) lead to massive transport of sediment particles and can, to a lesser extent, enhance porewater transport (Richard et al. 2023). The bioturbation

generated by the clam can affect the biomass of benthic primary producers, the density of functionally important co-occurring species, sediment stability and nutrient cycling (Soares and Sobral 2009, Clare et al. 2016, Van Colen et al. 2020, Richard et al. 2023). Several trematode species are known to infect *S. plana*, acting as both a first and second intermediate host (Desclaux 2003, Dairain et al. 2019 for reviews) but metacercariae of the genus *Himasthla* are the most prevalent and abundant in *S. plana* along the French English Channel coastlines (pers. obs.). Metacercariae are observed in the foot and siphons (pers. obs.), which are two of the main organs involved in bivalve bioturbation activity (Hughes 1969, Van Colen et al. 2020, Richard et al. 2023). We thus hypothesized that *Himasthla* spp. could significantly interfere with the feeding and sediment reworking activities of *S. plana*, with potential consequences for remineralization processes and nutrient fluxes across the SWI, and that this effect could be density-dependent.

Material and methods

Collection of *Scrobicularia plana* and sediments, and acclimation

Adult peppery furrow shell *S. plana* of similar size (total length = 30.5 ± 0.05 , mean \pm SE) were sampled by hand in May 2022 at two sites (Le Guillec and Saint-Brieuc) along the north Brittany coast (Table 1). Peppery furrow shells are abundant at both Le Guillec and Saint-Brieuc and densities can reach 212 ind. m^{-2} (Ponséro et al. 2021). These two sites are small estuaries located at the same latitude. Granulometry was similar at the two sites and consisted of muddy sand. We chose to evaluate the density-dependent effect of trematode parasites *Himasthla* spp. on the bioturbation activity of *S. plana* using environmentally parasitized bivalves to assess the natural effect of parasite infection on the host (versus experimentally induced infection). A prospection survey conducted in winter 2021–2022 showed that parasite abundances in *S. plana* ranged from 0 to 226 (mean \pm SE = 35.6 ± 3.3 ; $n=120$) and 1 to 70 *Himasthla* spp. per individual at Le Guillec and Saint-Brieuc (mean \pm SE = 16.5 ± 0.72 ; $n=186$), respectively. Considering that Le Guillec and Saint-Brieuc show similar environmental characteristics, bivalves were sampled at these two sites to ensure the widest range of infection rate between bivalves.

Once collected, bivalves were immediately transported to the laboratory where they were maintained in small tanks containing sediments (height of sediment column: ca 8 cm) and oxygenated unfiltered seawater. Organisms were exposed to semi-diurnal emersion–immersion cycles of 7:30:4:30 h

to mimic environmental tidal periods. Bivalves were left to acclimatize to experimental tidal conditions for five days before being introduced to the experimental units (section ‘Experimental set-up’). The seawater temperature and salinity during the acclimation period were 34.2°C and 14.2, respectively.

Muddy sand sediments were collected at Le Guillec. They were sieved through a 1 mm mesh to remove macrofauna and debris, homogenized and then placed in the experimental units. The units consisted of PVC tubes (internal diameter = 9.4 cm, height = 22 cm) and were filled with 21 cm of homogenized sediment. Experimental units were pre-incubated for three weeks in an air-saturated seawater open circuit to stabilize the sediment matrix and restore near-steady conditions after sediment homogenization. Sediment characteristics were: sand = 83.6%, mud = 16.4%, organic matter = 4.8% and median grain size $D_{50} = 167.1 \mu\text{m}$.

Experimental set-up

Following the pre-incubation period (section ‘Collection of *Scrobicularia plana* and sediments, and acclimation’), experimental units were transferred into a 500 l mesocosm with a semi-diurnal tidal cycle of 7:30:4:30 h emersion–immersion periods (one diurnal emersion phase). Air-bubbling systems were added to the mesocosm to keep the unfiltered water fully oxygenated during the eight days of the incubation period. On day 1, one peppery furrow shell (mean total length \pm SE = 30.5 ± 0.2 mm; $n=24$) was added to each experimental unit (corresponding density of bivalves = 144 ind. m^{-2}) early during diurnal low tide. On day 2, 7 g of inert particles fluorescing under UV light (‘luminophores’; size range = 100–160 μm , density = 2.6 g cm^{-3}) were homogeneously spread at the sediment surface of the experimental units early during the diurnal emersion period to estimate subsequent particles’ transport. On the same day, and early into the following immersion period, ca 500 g of sodium bromide (NaBr, MM = $102.89 \text{ g mol}^{-1}$) was introduced into the water column of the tidal mesocosm to estimate solute transport. The natural background concentration of bromides in the seawater was 0.88 mM and reached 10.2 mM after the enrichment. The incubation experiment consisted of 30 total units; twelve units for each sampling site (Le Guillec and Saint-Brieuc), and six ‘Control’ units that did not contain any bivalves. The seawater temperature and salinity during the experimental period were the same as during the acclimation period (section ‘Collection of *Scrobicularia plana* and sediments, and acclimation’).

Nutrient flux analysis

After seven days (from day 2 to 8 of the experimental incubation period), the exchange rates of ammonium (NH_4^+),

Table 1. Coordinates of the two intertidal sampling sites along the north Brittany coast, France, where specimens of *Scrobicularia plana* were sampled, and the mean abundance (\pm SE) of parasites *Himasthla* spp. counted in the tissues of the bivalves at the end of the experiment.

Site	Coordinates	Parasite abundance (mean no. of metacercariae \pm SE)
Le Guillec	48°40'46"N, 4°03'41"W	15.6 ± 4.2 ($n=11$)
Saint-Brieuc	48°30'52"N, 2°40'40"W	32.9 ± 6.4 ($n=11$)

nitrite and nitrate (NO_2^- and NO_3^-), phosphate (PO_4^{3-}), dissolved silicates (dSi) and dissolved oxygen (O_2) at the SWI were assessed over an additional incubation period. An incubation chamber (diameter = 10 cm, volume = ca 500 ml) was added to the top of each experimental unit, along with water from the tidal mesocosm. An oxygen probe was placed in the water column through the lid of the incubation chamber. A magnetic stirrer was used to homogenize the water column. Incubations ran for up to 3 h and were stopped before the O_2 level reached < 80%. The 0 and 100% oxygen calibrations were performed in a sodium ascorbate solution and in the saturated overlying water of the incubation core before the beginning of the incubation, respectively. We sampled 50 ml of water at the start and the end of the additional incubation period to quantify nutrient concentrations. A continuous flow analyser was used to measure dissolved concentrations of NO_3^- , NO_2^- , PO_4^{3-} and dSi, and a fluorimeter was used for NH_4^+ . Oxygen and nutrient fluxes (net emission or consumption rates) were calculated as the difference between initial and final concentrations in the water column relative to the duration of the incubation.

Bioturbation analyses

Following measurements of nutrient fluxes at the SWI (section 'Nutrient flux analysis'), the 1) concentration of NaBr in porewater along depth and 2) vertical distribution of luminophores (section 'Abundance of parasites in the bivalve samples') were determined in each experimental unit. Sediment cores were sliced in 0.5 cm layers from the surface to 5 cm depth and in 1 cm layers from 5 to 15 cm depth. During slicing, bivalves were sampled and stored with seawater pending dissection for parasite pressure quantification (section 'Data analysis').

Bioirrigation analysis

Sediment samples (20 slices per experimental unit) were centrifuged (4000 rpm for 10 min) to extract porewater. This was then sampled and filtered over a 0.22 μm cellulose acetate filter. NaBr concentrations in porewater along the sediment column were quantified following Presley (1971). Briefly, bromides were oxidized using chloramine-T in the presence of phenol red and acetate buffer. Absorbance of the samples was then measured spectrophotometrically ($\lambda = 595$ nm) and bromide concentrations were calculated using a standard curve.

Measured vertical profiles of bromide concentration in porewater along depth were used to estimate the non-local exchange coefficient of bioirrigation α (year^{-1}) (Andersson et al. 2006) by mathematically fitting the latter to a non-local transport model according to:

$$\frac{\partial C}{\partial t} = D_s \frac{\partial^2 C}{\partial z^2} + \alpha(C_{\text{ow}} - C_z)$$

with C denoting the concentration of bromide in the overlying water (C_{ow}) and at depth (C_z), t the time (year), D_s the

molecular diffusivity and α the non-local exchange coefficient of bioirrigation α (year^{-1}). Vertical profiles of bromide concentration in control units (i.e. without bivalves) were used to determine the molecular diffusive transport D_s of the tracer (Boudreau 1986a, François et al. 2002). Accuracy of the numerical simulation was based on a least square method as well as on visual inspection of similarity between predicted and real vertical profiles of the tracer.

Sediment particle mixing analysis

Following porewater extraction, sediment samples (20 slices per experimental unit) were frozen and freeze dried. Then, each sample was gently sieved over a 1 mm mesh and homogenized. A subsample of 2 g was dispersed over a Petri dish before it was photographed under UV light using a digital camera fitted with a yellow filter. Luminophores in each slice were semi-automatically counted using a custom program we built that counted luminophore pixels after a binarization step (based on the RGB level), which allowed computation of 1-dimensional (1-D) vertical profiles of the relative percentage of luminophores at each depth. From these, the biodiffusion D_b ($\text{cm}^2 \text{year}^{-1}$) and bioadvection v_b rates ($\text{cm}^2 \text{year}^{-1}$) were estimated by fitting vertical profiles with a 1-D gallery-diffusor model (François et al. 2002). The goodness of fit of the simulation was estimated by visual inspection of similarity between predicted and real vertical profiles of luminophores and by using the least square method.

Abundance of parasites in the bivalve samples

Organisms were dissected to determine the abundance of trematodes *Himasthla* spp. in their tissues. The posterior adductor muscle of each bivalve was cut to open the shell, and all soft tissues were removed and squeezed between two glass plates. Then, trematode metacercariae were counted using an inverse stereomicroscope. Last, bivalves' soft tissues were dried for at least 48 h at 60°C and weighed (dry weight, DW). Condition indices of the bivalves were calculated as the ratio of DW (mg) to shell weight (g).

Data analysis

A Student t-test was used to test for differences in the condition index of the bivalves between the two sampling sites (Le Guillec versus Saint-Brieuc). The relationship between the condition index of the bivalves and the abundance of trematodes *Himasthla* spp. in their tissues was estimated using a linear regression. Analysis of covariance was applied to test for differences in the relationship between these two variables across sampling sites.

The effect of *S. plana* on 1) sediment particle transports (i.e. luminophore maximal penetration depth, biodiffusion D_b and bioadvection v_b coefficients), 2) porewater transports (i.e. maximal penetration depth of bromide in the sediment column and non-local exchange coefficient of bioirrigation α) and 3) nutrient fluxes at the SWI was evaluated using a Student t-test or a Wilcoxon test when assumptions were not

met. When a significant effect of the bivalves on sediment particle transports, porewater transports or nutrient fluxes at the SWI was observed, the density-dependent effect of parasitism was evaluated by conducting a linear (Pearson coefficient) or non-linear (Kendall coefficient) correlation analysis. Analysis of covariance was used to test for differences in the linear relationship between two variables across sampling sites.

Shapiro–Wilk and Bartlett tests were used to evaluate normality of the data and homogeneity of variances, respectively. When conducting regression analysis, normality of residuals and equal error variances were checked graphically. The null hypothesis was rejected when p -value < 0.05 . All statistical analyses were carried using R (ver. 4.1.1) (www.r-project.org).

Results

One bivalve died during the experiment, and another was infected with *Gymnophallus minutus* sporocysts. They were then excluded from the rest of the analyses. Eleven replicates were thus available from each site (Le Guillec and Saint-Brieuc).

Parasite abundance in bivalves

Metacercariae of the trematodes *Himasthla* spp. were observed in the foot and, to a lesser extent, in the siphons of *S. plana*. Abundances of *Himasthla* spp. ranged from 0 to 50 and from 6 to 62 per bivalve at Le Guillec and Saint-Brieuc, respectively (Table 1).

The condition indices of the bivalves sampled ranged from 57.8 to 156.8 and from 76.3 to 143.6 at Le Guillec and Saint-Brieuc sites, respectively, and there was no significant difference between the two sampling sites (Student t -test, $t=0.98$, p -value = 0.34), suggesting that bivalves were in similar physiological condition at the two sites. Overall, we observed a significant decline in the condition indices of bivalves with increasing numbers of trematode parasites (Fig. 1; linear regression, $R^2 = 0.36$, p -value < 0.01). This relationship was not affected by the sampling origin of the bivalves (ANCOVA, $F=0.13$, p -value = 0.73).

Effect of parasitism on the sediment reworking activity of *Scrobicularia plana*

In the control units without bivalves, luminophores remained in the uppermost sediment layer (Fig. 2). In contrast, we observed a global exponential decline in the relative abundance of luminophores along depth in units inhabited by *S. plana* with some subsurface peaks (Fig. 2). Bivalves transported surficial particles in the sediment column to an average maximal penetration depth (MPD) of 7.5 ± 0.7 cm (mean \pm SE) whereas MPD was 0.25 cm in control units (Student t -test, $t=10.6$, p -value < 0.01). Mathematical simulations confirmed this pattern with biodiffusion rates D_b significantly higher in the presence of *S. plana* than without ($D_b = 78.4 \pm 2.9 \cdot 10^{-3}$ versus $11.7 \pm 0.4 \cdot 10^{-3}$ cm² year⁻¹ (mean

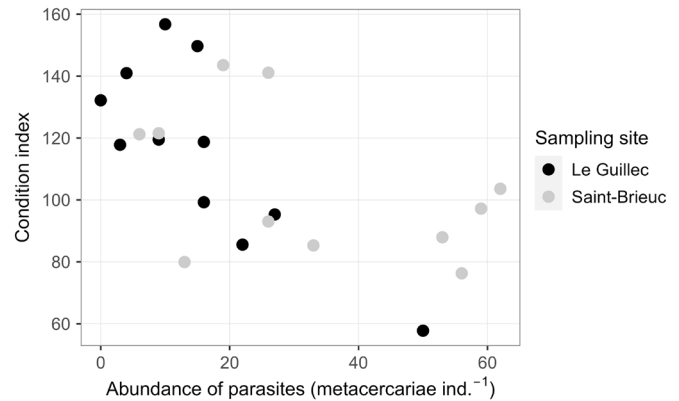


Figure 1. Condition index of bivalves *Scrobicularia plana* sampled at two sites (Le Guillec and Saint-Brieuc) along the north Brittany coast, France, as a function of parasite load with trematodes *Himasthla* spp.

\pm SE), respectively; Wilcoxon test, $W=112$, p -value < 0.01). Similarly, biotransport rates v_b were estimated to be 13.1 ± 3.4 cm² year⁻¹ (mean \pm SE) and null with and without *S. plana*, respectively (Wilcoxon test, $W=136$, p -value < 0.01).

Overall, the type of sediment transport generated by *S. plana* (Fig. 2) and its intensity (Fig. 3) depended on the abundance of parasites. We observed subsurface peaks of luminophores at shallower depths when the parasite burden was high in *S. plana* (Fig. 2). Moreover, both the MPD of luminophores in the sediment column (Fig. 3a) and the biotransport rate (Fig. 3c) significantly decreased with an increase in the number of *Himasthla* spp. in bivalve tissues (linear regressions, $R^2 = 0.31$, p -value < 0.01 and $R^2 = 0.22$, p -value < 0.05 , respectively). Those relationships were not affected by the sampling origin of the bivalves (ANCOVA, $F=0.02$, p -value = 0.89; and $F=2.1$, p -value = 0.16 for the MPD of luminophores and biotransport rate, respectively). In contrast, there was no significant correlation between the biodiffusion rate and the parasite load in the bivalves (Fig. 3b; Kendall's test, p -value = 0.84).

Effect of parasitism on the bioirrigation activity of *Scrobicularia plana*

We observed an exponential decline in the concentration of bromide in porewater with depth in units with and without bivalves (Fig. 4). Nonetheless, bivalves clearly stimulated the penetration of solutes in the sediment to deeper horizons as compared to the control units and, after seven days of incubation, tracers had penetrated to 11.7 ± 0.5 and 8.6 ± 0.2 cm (mean \pm SE) deep in the sediment with and without *S. plana*, respectively (Wilcoxon test, $W=132.0$ and 16.9 , p -value < 0.01). There was also a significant non-local transport of water in the sediment column inhabited by bivalves as compared to the control, with the non-local exchange coefficient α averaging 5.4 ± 0.9 year⁻¹ (mean \pm SE) (Student t -test, $t=11.1$, p -value < 0.01).

The influence of bivalves on porewater transport depended on parasitic burden (Fig. 5). There was a significant negative

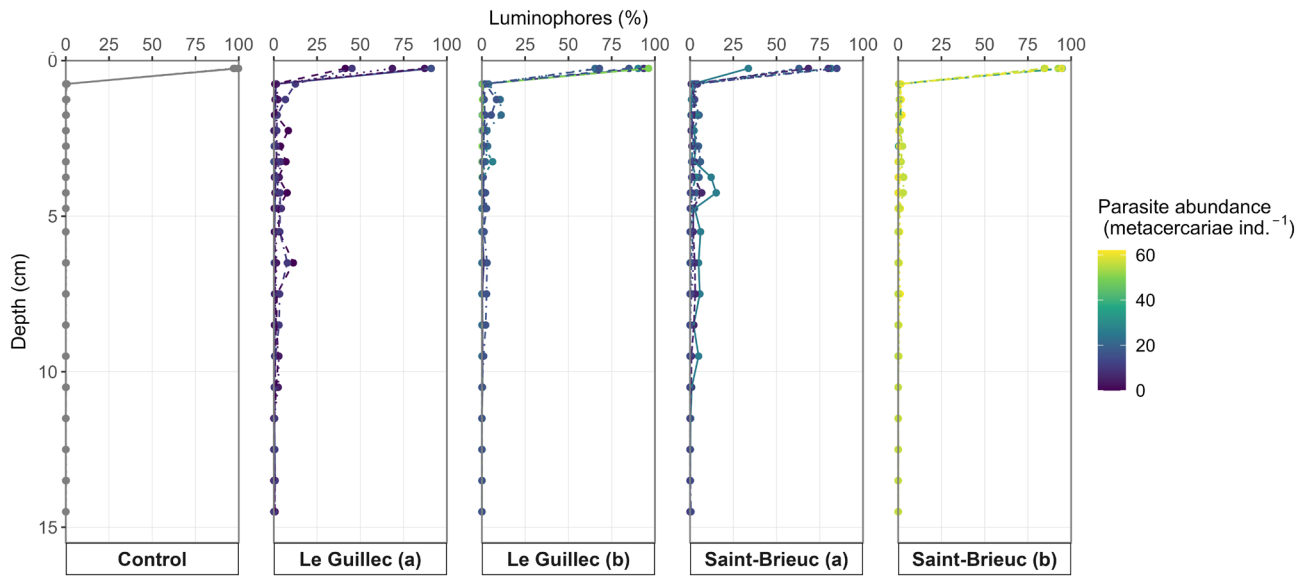


Figure 2. Vertical distribution of fluorescing inert particles ('luminophores') along depth in experimental units inhabited by bivalves *Scrobicularia plana* collected at two sampling sites (Le Guillec and Saint-Brieuc) to ensure contrasted parasite infection rates by metacercariae of trematodes *Himasthla* spp. (n=11 replicates per site). To facilitate readability, bivalves from each site were separated into two sub-groups depending on parasite burden (Le Guillec (a) and Le Guillec (b); Saint-Brieuc (a) and Saint-Brieuc (b)). 'Control': experimental units without any bivalves.

correlation between the maximal penetration depth of bromides and the abundance of parasites in *S. plana* (Fig. 5a; Kendall's test, $\tau = -0.52$, p-value < 0.001). Similarly, we observed a decline in the non-local exchange coefficient α with an increase in the number of trematodes parasitizing *S. plana* (Fig. 5b; linear regression, $R^2 = 0.30$, p-value < 0.01). This relationship was not significantly affected by the origin of the bivalves (ANCOVA, $F = 1.17$, p-value = 0.29).

Effect of parasitism on nutrient fluxes across the sediment–water interface

There was a 2.4-fold increase in the sediment total oxygen uptake (Wilcoxon test, $W = 110$, p-value < 0.01) and 8.6-fold and 2.1-fold increases in effluxes of ammonium NH_4^+ (Wilcoxon test, $W = 132$, p-value < 0.01) and nitrite NO_2^- (Student t-test, $t = 3.9$, p-value < 0.01), respectively, when *S. plana* was present (Supporting information). Net phosphate PO_4^{3-} fluxes were almost null without *S. plana* whereas there was a net efflux from the sediment to the water column in the presence of bivalves (Supporting information; Wilcoxon test, $W = 132$, p-value < 0.01). In contrast, the peppery furrow shell did not significantly affect nitrate NO_3^- (Supporting information; Wilcoxon test, $W = 41$, p-value = 0.92) nor dissolved silicate dSi (Supporting information; Wilcoxon test, $W = 71$, p-value = 0.40) fluxes across the SWI.

There was no significant density-dependent effect of parasites *Himasthla* spp. on nutrient fluxes across the SWI (Fig. 6). We did not observe any significant correlation between the number of parasites hosted by *S. plana* and the fluxes of 1) oxygen (Fig. 6a; Kendall's test, $\tau = 0.17$, p-value = 0.28), 2) NH_4^+ (Fig. 6b; Kendall's test, $\tau = -0.17$, p-value = 0.28), 3)

NO_2^- (Fig. 6c; Kendall's test, $\tau = -0.02$, p-value = 0.91) and 4) PO_4^{3-} (Fig. 6d; Kendall's test, $\tau = -0.18$, p-value = 0.24).

Discussion

Parasitism as an influential determinant of bioturbation processes

In coastal soft-bottom environments, bioturbation constitutes an archetypal example of ecosystem engineering (Meysman et al. 2006, Kristensen et al. 2012). Through their activities, some benthic organisms disproportionately influence the transport of particles and porewater solutes within the sediment column (Kristensen et al. 2012), with profound effects on its physical (Rhoads and Young 1970, Jones and Jago 1993) and biogeochemical (Aller 1982) properties. This has important implications for the functioning of those environments, including modulation of sediment stability (Le Hir et al. 2007, Orvain et al. 2007), nutrient regeneration processes (Lohrer et al. 2004, Pascal et al. 2016) and benthic community structure (Mermillod-Blondin et al. 2004, Pillay and Branch 2011). Here, we confirmed the importance of *S. plana* as one of these organisms. This endobenthic bivalve generates intense sediment mixing and, to a lesser extent, stimulates solute transports in the sediment column. As a result, the clam bioturbation activity enhances nutrient fluxes across the SWI and organic matter remineralization, as already shown by Richard et al. (2023).

The extent to which bioturbators can act as allogenic ecosystem engineers depends on the organisms' abundance (or biomass) (Dupont et al. 2006, Cozzoli et al. 2018), physiological state (Dairain et al. 2020, Przeslawski et al. 2009) and the

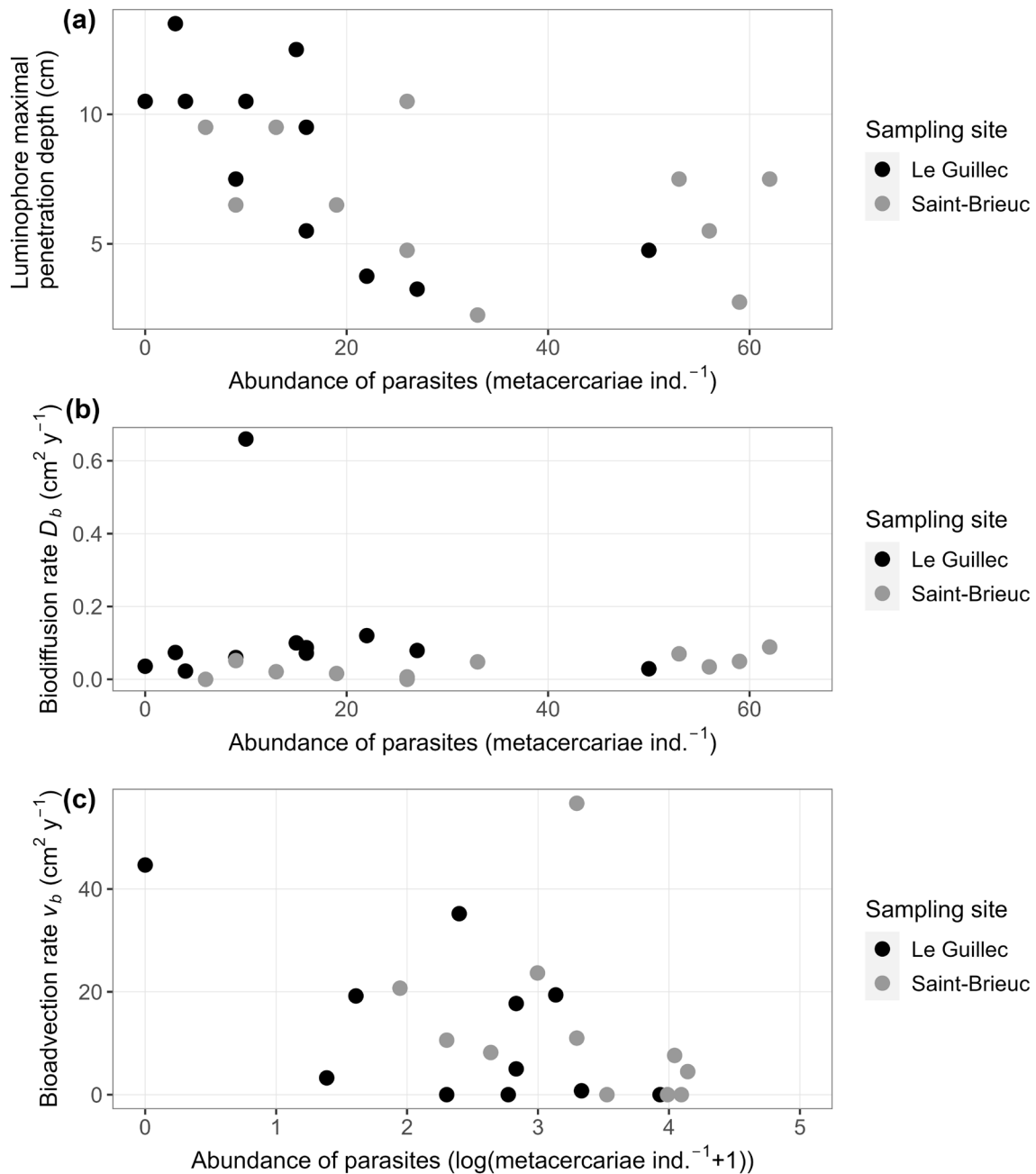


Figure 3. Influence of bivalves *Scrobicularia plana* on (a) the maximal penetration depth of fluorescing particles ('luminophores') in experimental sediment columns (cm), (b) the estimated biodiffusion rate D_b (cm² year⁻¹) and (c) the estimated bioadvection rate v_b (cm² year⁻¹) as a function of parasite load with trematodes *Himasthla* spp. per individual *S. plana*. Bivalves were collected at two sampling sites (Le Guillec and Saint-Brieuc) to ensure contrasted parasite burdens.

type and intensity of their activity (Mermillod-Blondin et al. 2004, Pascal et al. 2016). Several abiotic and biotic factors, including interspecific interactions (Mermillod-Blondin et al. 2005, Maire et al. 2010, Premo and Tyler 2013, Clare et al. 2016), can influence the behaviour and activities of bioturbators. The present results add to the mounting evidence of the potential of parasitic interactions to alter phenotypic traits of bioturbating organisms that influence their ecosystem engineering role (Mouritsen and Haun 2008, Simão et al.

2010, Dairain et al. 2020, Pascal et al. 2020). The intensity of both sediment reworking and bioirrigation activities of *S. plana* decreased with an increase in the number of trematode parasites *Himasthla* spp. within the host, and parasite burden can explain up to 31% of the inter-individual behavioural variability. Additionally, when the bivalves were heavily parasitized, the intensity of their sediment reworking activity was almost null, suggesting a strong threshold effect. In addition to negatively affecting the intensity of the

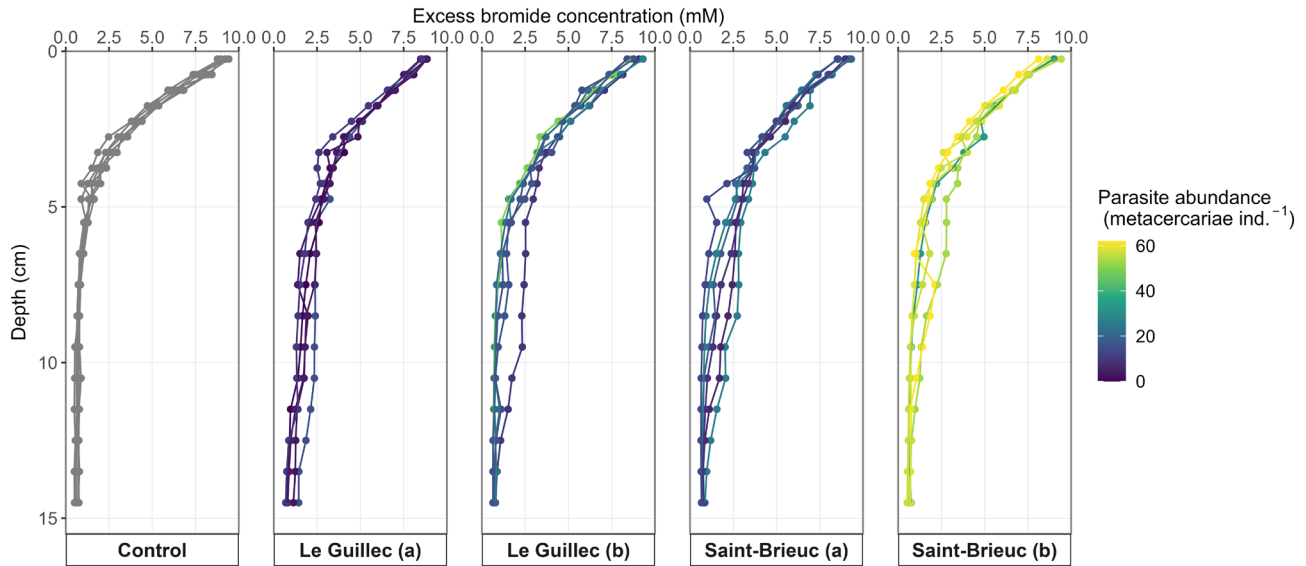


Figure 4. Vertical profiles of sodium bromide concentrations in porewater along depth in experimental units inhabited by bivalves *Scrobicularia plana* naturally parasitized by different numbers of metacercariae of trematodes *Himasthla* spp. and without any bivalves ('Control'). Bivalves were collected at two sampling sites (Le Guillec and Saint-Brieuc) to ensure contrasted parasite burdens. To facilitate readability, specimens from each site were separated into two sub-groups depending on parasite burden (Le Guillec (a) and Le Guillec (b); Saint-Brieuc (a) and Saint-Brieuc (b)). 'Control': experimental units without any bivalve.

clams' reworking activity, parasites also affected their mode of particle transport. Bivalves weakly parasitized by trematodes *Himasthla* spp. (i.e. infection intensity ranging from 0 to 27 metacercariae per specimen) generated both local and non-local transports of sediment particles, by displacing sediment material between non-adjacent areas, whereas more heavily parasitized clams only generated biodiffusive-like particle transports, where sediment particles were moved over short distances in a random manner (Boudreau 1986a, b). In other words, non- or weakly infected *S. plana* behaved as downward conveyors, while more heavily infected clams turned into biodiffusers (François et al. 1997). Such changes in the functional type of sediment mixing could be explained by alterations in the bivalve mobility and feeding activity. There was a negative correlation between the MPD depth of luminophores in the sediment and the number of *Himasthla* spp. in the bivalves' tissues. The more heavily infected the bivalves were, the shallower they were in the sediment column, suggesting that intense parasitic infection impairs their burrowing capacity. Nevertheless, the alteration of the burrowing capacity of highly infected *S. plana* alone cannot explain the differences in vertical luminophore distributions (i.e. number and depths of sub-surface peaks), since the tracers were added once bivalves were buried, and buried *S. plana* show little vertical migration within the sediment column (Zwarts and Wanink 1989, Cardoso et al. 2010). Therefore, we suggest that reduced deposit-feeding rates of heavily infected bivalves could also contribute to this functional change. The inhalant and exhalant siphons occupy semi-permanent burrows, and downward non-local transport of sediment particles could occur when 1) the bivalve retracts or extends its siphons to feed at the sediment surface (Hughes 1969) and

2) claps its valves following feces expulsion (Van Colen et al. 2020). Therefore, the lower potential of heavily infected organisms to stimulate porewater transport might also partially be due to the detrimental effects of *Himasthla* spp. on the deposit feeding activity of its hosts, since water transports in the sediment column are clearly induced by bivalve siphon movements and valve claps (Wetthey and Woodin 2005, Woodin et al. 2016).

Whether we assume that the density-dependent negative effects of trematodes *Himasthla* spp. on *S. plana* bioturbation is a consequence of parasites reducing the feeding and, to a lower extent, locomotion activities of the bivalve, the underlying mechanisms are still unknown. Nonetheless, we can formulate two assumptions. First, we observe a negative correlation between the condition index of *S. plana* and parasitic burden, with parasite load explaining 36% of the inter-individual variability. The deleterious effects of parasites on the magnitude of bioturbation capabilities of *S. plana* might be a side effect of the infection altering the overall physiological state of the bivalve. Second, trematode parasites were observed to infect the foot and the siphons of the bivalve. These two organs are involved in the locomotion/burrowing and feeding activities, respectively, of *S. plana*. In cockles *Austrovenus stutchburyi*, the presence of trematodes from the Himasthidae family in the bivalve foot could reduce its growth (Thomas and Poulin 1998) and greatly interfere with its ability to contract (Mouritsen 2002). By impairing the growth of the siphons and foot of *S. plana* and/or lowering the ability of these muscular organs to contract, *Himasthla* spp. may affect critical functional traits of the bivalve, with direct and profound consequences for engineering processes such as sediment bioturbation.

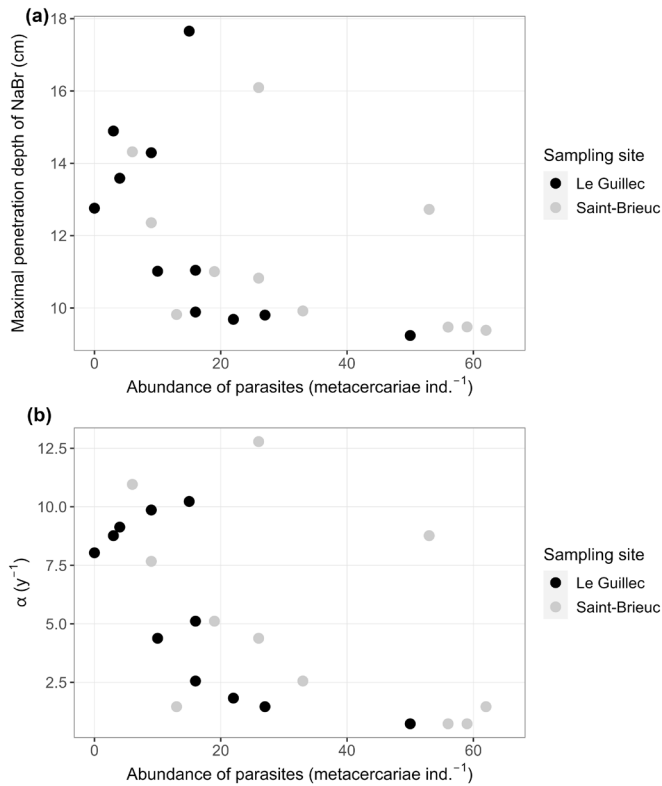


Figure 5. Influence of bivalves *Scrobicularia plana* on (a) the maximal penetration depth of sodium bromide (NaBr) in experimental sediment columns (cm) and (b) the estimated non-local exchange coefficient of bioirrigation α (year⁻¹) as a function of parasite load with metacercariae of trematodes *Himasthla* spp. per individual *S. plana*. Bivalves were collected at two sampling sites (Le Guillec and Saint-Brieuc) to ensure contrasted parasite burdens.

Costs of indirect trait-mediated effects of parasitism for ecosystem processes

The bioturbation activity of *S. plana* decreased with an increase in the number of *Himasthla* spp. metacercariae hosted by the bivalve. Nonetheless, our study suggests that this trend did not significantly impact nutrient cycling. We measured biogeochemical exchanges across the SWI (as a proxy of nutrient cycling) and showed that bivalves stimulated sediment oxygen uptake and efflux of ammonium, nitrite and phosphate, irrespective of their parasite burden. This pattern, surprisingly, differs from results obtained by others (Simão et al. 2010, Pascal et al. 2020). For instance, the bopyrid parasite *Gyge branchialis* reduces the sediment reworking and bioirrigation activities of the mud shrimp *Upogebia pusilla* by a factor of approximately 5 and 3, respectively. This leads to a 1.5-fold decrease in sediment oxygen uptake, 1.9 and 6.4-fold decreases in emissions of ammonium and dissolved silicates in the water column and a 6.4-fold decrease in nitrite fluxes from the water to the sediment (Pascal et al. 2020). Mud shrimp are deep-burrowing bioturbators living in large and extended burrows that are actively ventilated (Pillay and Branch 2011). In contrast, burrows of clams such as the peppery furrow shell are restricted to the

immediate vicinity of the shell and siphons (Hughes 1969, Zwartz and Wanink 1989), and clams thus generate relatively low porewater transports. Both sediment reworking and bioirrigation processes can greatly influence microbial community structure, functioning and benthic mineralization processes (Mermillod-Blondin et al. 2004, Papaspyrou et al. 2007, Bertics and Ziebis 2009). Yet, intense bioirrigators exhibit a more significant influence on biogeochemical processes than organisms with low bioirrigation rates and high sediment mixing activity (Mermillod-Blondin et al. 2004, Michaud et al. 2006, Quintana et al. 2007, Richard et al. 2023). Therefore, bioirrigation is likely the main process influencing nutrient exchange across the SWI. *Scrobicularia plana* initiates small solute transports, so changes to the bioirrigation behaviour of *S. plana* caused by the presence of trematodes *Himasthla* spp. might not significantly impact nutrient fluxes, as the bivalve's bioirrigation capabilities may have been too low to detect any cascading effects of parasitism. On the other hand, we suggest that sediment reworking and bioirrigation might also influence microbial processes at two different timescales, with bioirrigation being 1) a less irregular activity than sediment reworking and 2) a shorter-term process affecting nutrient cycling. In our opinion, the duration of incubations conventionally conducted to quantify nutrient exchanges across the SWI (i.e. typically a few hours) might be too short to detect changes in nutrient fluxes and effects on organic matter remineralization rate caused by sediment particle transports. Although we detected a negative effect of the parasite load on *S. plana* bioirrigation and sediment reworking activities, methodological limitations may have constrained our ability to accurately estimate the importance of parasitism on the role of *S. plana* in nutrient regeneration dynamics.

Even though the indirect trait-mediated effects of *Himasthla* spp. on *S. plana* did not cascade down on biogeochemical exchanges at the SWI in our short-term incubation experiment, other repercussions at the community and ecosystem levels should not be excluded. For instance, *S. plana* can negatively affect the density and activity of other common benthic macro-organisms that also act as ecosystem engineers (Clare et al. 2016). These structuring roles were thought to be a result of the feeding and biodeposition of *S. plana*. One may hypothesize that, by reducing the ability of clams to mix the sediment matrix, trematode parasites may modulate the abundance and functional importance of co-occurring species. In fact, such an indirect structuring role of parasites in marine soft-bottom communities has been reported by Mouritsen and Poulin (2005) using a taxonomically similar host (endobenthic bivalve)–parasite (trematode metacercaria) association. By carrying out field experiments to evaluate trait-mediated effects of the trematode *Curtuteria australis* on the structure of benthic community dominated by the New Zealand cockle *Austrovenus stutchburyi*, they showed that, in areas colonized by heavily parasitized cockles, the sediment surface was significantly less reworked as a result of the parasite interfering with the mobility of its host. One of the reported consequences was an increase in

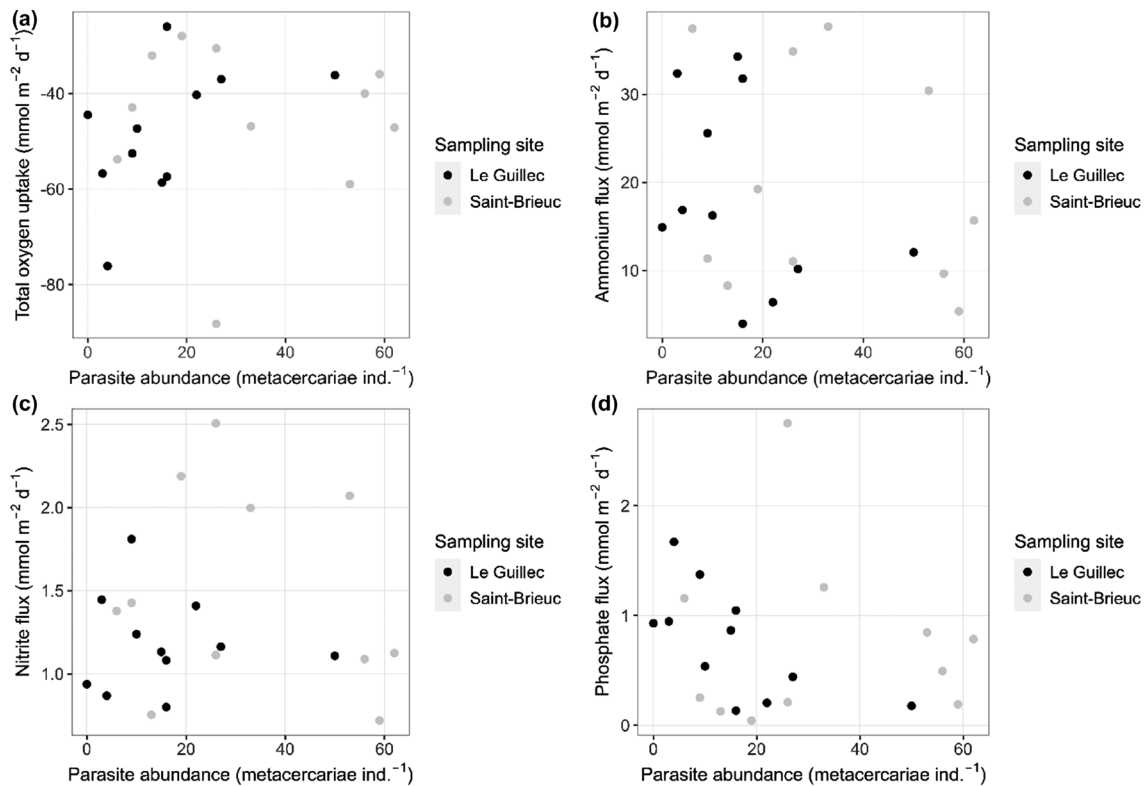


Figure 6. Influence of the bivalve *Scrobicularia plana* on (a) the total oxygen uptake from the water column to the sediment, (b) ammonium NH_4^+ efflux, (c) nitrite NO_2^- efflux and (d) phosphate PO_4^{3-} efflux at the sediment–water interface as a function of parasite load with metacercariae of trematodes *Himasthla* spp. per individual *S. plana*. Bivalves were collected at two sampling sites (Le Guillec and Saint-Brieuc) to ensure contrasted parasite burdens. None of the correlations between the nutrient fluxes and the abundance of parasites in *S. plana* were statistically significant (ANCOVA).

macroinvertebrate species richness and abundance, as well as concomitant changes in the taxonomic composition of the benthic community. The functioning of the community might also have been affected, as some functional groups – such as deposit-feeders and grazers – benefited more than others from the parasite-induced relaxed disturbance of the benthic interface.

In addition to the potential modulation of the structuring role of *S. plana* on the associated benthic community, trematodes of the genus *Himasthla* may also be potent determinants of ecosystem processes by influencing sediment dynamics. Indeed, the bioturbation and feeding activities of *S. plana* can deconsolidate sediments and affect the roughness of the SWI, thus increasing sediment sensitivity to hydrodynamic forcing (Orvain et al. 2007, Soares and Sobral 2009). The indirect effect of parasites on sediment roughness, and thus resistance to erosion, has recently been measured using the bivalve–trematode *Cerastoderma edule*–*Bucephalus minimus* association (Dairain et al. 2020) and might also be envisaged for the *S. plana*–*Himasthla* spp. system.

Conclusion

Parasites are ubiquitous components of marine ecosystems and play a major role in biodiversity-mediated processes

through the effects they exert on critical hosts like ecosystem engineers. In coastal soft-bottom environments, bioturbating organisms are one major group of ecosystem engineers that greatly influence central ecological processes, but only a few studies have assessed the impact of parasites on the functional activity of these organisms (Mouritsen and Poulin 2005, Mouritsen and Haun 2008, Dairain et al. 2020, Pascal et al. 2020). Using an ex situ experimental approach, we showed that trematode parasites can significantly impair the bioturbation activity of the bivalve *S. plana* in a density-dependent way. Parasite-induced changes to functional activities of the host did not affect fluxes of nutrients at the sediment interface over a short temporal scale, i.e. a few hours during which the bioirrigation process dominates. However, we cannot exclude significant impacts on nutrient regeneration at longer time scales during which the effects of both bioirrigation and particle reworking processes can be observed. Finally, other wide indirect trait-mediated effects of parasites may also occur and should be assessed. In particular, we chose to evaluate the influence of parasitism on the physiology and behaviour of an ecosystem engineer using a simple experimental approach, and only focused on individual *S. plana* maintained in defaunated experimental units. We thus did not account for potential direct and indirect interactions of the bivalve with other members of the benthic community, including other *S. plana*. To have a better mechanistic

understanding of the whole potential of trematode parasites to influence the functioning of benthic communities dominated by bioturbating engineers, longer-term integrative ex situ and in situ experimental work combining behavioural studies, community ecology approaches and quantification of ecosystem processes should be conducted. Such studies would generate an essential baseline to realistically assess, and ultimately predict, how disturbance – including on-going global change – may affect engineer–parasite interactions, and ultimately the dynamics of these systems.

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Author contributions

Annabelle Dairain: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Software (equal); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead). **Manon Doutrelant:** Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Sarah Bureau:** Data curation (supporting); Formal analysis (equal); Methodology (equal); Writing – review and editing (supporting). **Sébastien Henry:** Methodology (equal); Writing – review and editing (supporting). **Olivier Maire:** Funding acquisition (equal); Software (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5qfttdzd7> (Dairain et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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