

Macrofaunal irrigation traits enhance predictability of nutrient fluxes across the sediment–water interface

Alexa Wrede^{1,2,3,4,7,*}, Henrike Andresen^{1,3,6}, Ragnhild Asmus²,
Karen Helen Wiltshire^{1,2,5}, Thomas Brey^{1,2,4}

¹Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Am Handelshafen 12,
27570 Bremerhaven, Germany

²Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation Sylt, Hafenstraße 43,
25992 List, Germany

³Helmholtz Institute for Functional Marine Biodiversity at the University Oldenburg, Ammerländer Heerstraße 231,
26129 Oldenburg, Germany

⁴University Bremen, Bibliothekstraße 1, 28359 Bremen, Germany

⁵Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland,
Am Binnenhafen 1117, 27498 Helgoland, Germany

⁶Present address: Thünen Institute, Institute of Sea Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

⁷Present address: Helmholtz Zentrum Geesthacht Center for Materials and Coastal Research, Max-Planck Str. 1,
21502 Geesthacht, Germany

ABSTRACT: This study shows that macrofaunal irrigation traits constitute a valuable complement to sediment reworking traits in estimating macrofaunal impact on nutrient fluxes across the sediment–water interface. We correlated density, biomass, community bioturbation potential (BP_c , an index based on reworking traits, body mass and density) and community irrigation potential (IP_c , an index based on irrigation traits, body mass and density) with nitrite, nitrate, ammonium, silicate and phosphate flux data under different environmental conditions. Generalized linear models performed best with a combination of environmental conditions and irrigation trait-based indices. This was not only a direct effect of the irrigation traits, but also of the scaling factor 0.75 employed in IP_c to infer metabolic activity from body mass. Accordingly, predictive models of nutrient flux across the sediment–water interface will profit greatly from incorporating macrofaunal irrigation behaviour by means of trait-based indices.

KEY WORDS: Bioirrigation · Bioturbation · Functional traits · Ecosystem functioning

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1. INTRODUCTION

Benthic biogeochemical cycling and mineralisation processes are strongly promoted by macrofaunal activities such as sediment reworking (biomixing of sediment particles) and bioirrigation, i.e. ventilation and flushing of burrows (Aller 1994, Kristensen et al. 2012, Baranov et al. 2016). The scope of these activities depends largely on the functional characteristics and the size of the macrofaunal organisms. Accordingly, many studies have explored the predictability of biogeochemical cycling via body mass and macro-

faunal traits (Solan et al. 2004, Braeckman et al. 2010, Murray et al. 2014). A widely adopted example for a non-quantitative trait-based index is the community bioturbation potential (BP_c) of Solan et al. (2004) (Birchenough et al. 2012, Queirós et al. 2013, Gogina et al. 2017). BP_c includes biomass, density and sediment reworking traits (mobility and reworking type) (Solan et al. (2004)). The broad application of BP_c is thus useful, as it correlates with numerous biogeochemical parameters and processes, such as biogenic mixing depth, sediment oxygen consumption and denitrification (Birchenough et al. 2012, Braeck-

man et al. 2014, Gogina et al. 2017). However, nutrient fluxes across the sediment–water interface are also strongly dependent on the irrigative introduction of oxygenated water into anoxic areas of the sediment or the enhancement of pore water exchange through irrigation (Mermillod-Blondin et al. 2004, Braeckman et al. 2014, Wrede et al. 2017). Accordingly, the sediment reworking traits of BP_c may only partly describe macrofaunal impacts on nutrient flux across the sediment–water interface.

To account for the importance of bioirrigation, Wrede et al. (2018) proposed an alternative index, the community irrigation potential (IP_c), which is based on irrigation traits such as feeding type, burrow type and irrigation depth (Solan et al. 2004, Wrede et al. 2018). In a slightly different approach, Renz et al. (2018) confirmed the plausibility of these traits as bioirrigation proxies with a thorough literature review. In contrast to BP_c , IP_c based on macrobenthic ash-free dry mass (AFDM) shows a consistent correlation with macrofaunal irrigation activity across various sediment types and communities (Wrede et al. 2018). Yet, so far we lack confirmation that IP_c is also a suitable predictor of nutrient fluxes across the sediment–water interface. Moreover, there is a need to resolve the ambiguity in the use of macrofaunal body mass units between IP_c and BP_c . Whereas most studies use BP_c based on wet body mass (WM) (Braeckman et al. 2014, Gogina et al. 2017, Wrede et al. 2017), Wrede et al. (2018) demonstrated that bioirrigation correlates better with AFDM-based IP_c , as AFDM represents the biologically active part of an organism and is therefore a reasonable proxy of metabolic activity.

Accordingly, we hypothesised that irrigation traits as reflected in IP_c are suitable predictors of phosphate, silicate, ammonium, nitrate and nitrite fluxes across the sediment–water interface under different environmental conditions (i.e. sediment type, gradients across the sediment water column, temperature and faunal inventory) that constitute a valuable complement to sediment reworking traits (BP_c), density or biomass. Further, we hypothesised that both indices (BP_c and IP_c) predict nutrient fluxes better when calculated in AFDM.

2. MATERIALS AND METHODS

2.1. Dataset

We used data both from this study and a previous study on German Bight sediments (Wrede et al. 2017). The data encompassed biomass (WM and AFDM),

density, species identity, bioirrigation activity and nutrient flux measurements of nitrite, nitrate, ammonium, silicate and phosphate from laboratory incubations in different seasons (i.e. summer 2015 and spring 2016). We tested whether our first hypothesis, that IP_c is a suitable predictor of nutrient fluxes across the sediment–water interface, holds true across a variety of setups and conditions commonly used in bioturbation–nutrient flux studies (Hale et al. 2014, Murray et al. 2014). Firstly, we used artificial monocultures of organisms exhibiting different bioturbation behaviours and inhabiting different sediment types: mud: bivalve *Nucula nitidosa* Winckworth, 1930 and polychaete *Owenia fusiformis* Delle Chiaje, 1844; fine sand: brittle star *Amphiura filiformis* (O.F. Müller, 1776) and sea urchin *Echinocardium cordatum* (Pennant, 1777); and sand: polychaete *Lanice conchilega* (Pallas, 1766) and bivalve *Cerastoderma edule* Linnaeus, 1758 (Fig. 1, Table 1). For every sediment type, we included 5 control cores (cores without macrofauna). Secondly, we used corresponding natural communities inhabiting mud, fine sand and sand sediments (mud: *N. nitidosa*-community, Salzwedel et al. 1985; fine sand: *A. filiformis*-community, Salzwedel et al. 1985; sand: *L. conchilega*-reef, Rabaut et al. 2009).

2.2. Experimental procedure

Sediment, communities and experimental animals (for single-species experiments) were sampled from 3 different habitats in the German Bight (mud: 54°7'21"N, 8°12'96"E; fine sand: 54°0'50"N, 7°48'51"E; sand: 55°01'32"N, 8°26'10"E). The artificial monocultures were created by placing specimens of each species, according to their natural densities (Fig. 1), in rectangular cores (height: 35 cm, width: 9.4 cm, depth: 9.4 cm), filled with sieved (1 mm mesh) and homogenized sediment (18 ± 1 cm) that was left to settle for 4 d (summer 2015) or 8 d (spring 2016) before the beginning of the experiments (Wrede et al. 2017, 2018). In spring 2016, additional community experiments were conducted. Ten intact cylindrical sediment cores (height: 35 cm, depth: 9.4 cm) were taken from each location, i.e. in the intertidal directly from the sandflats, and in the subtidal from 0.1 m² box-core samples.

The cores with sediment and fauna were maintained at the Wadden Sea Station of the Alfred Wegener Institute on the island of Sylt with a continuous flow of filtered seawater (salinity of 28 ± 0.5 taken directly from the Sylt-Rømø Bight) and a 12:12 h light:dark cycle. The water temperature, salinity and nutrient

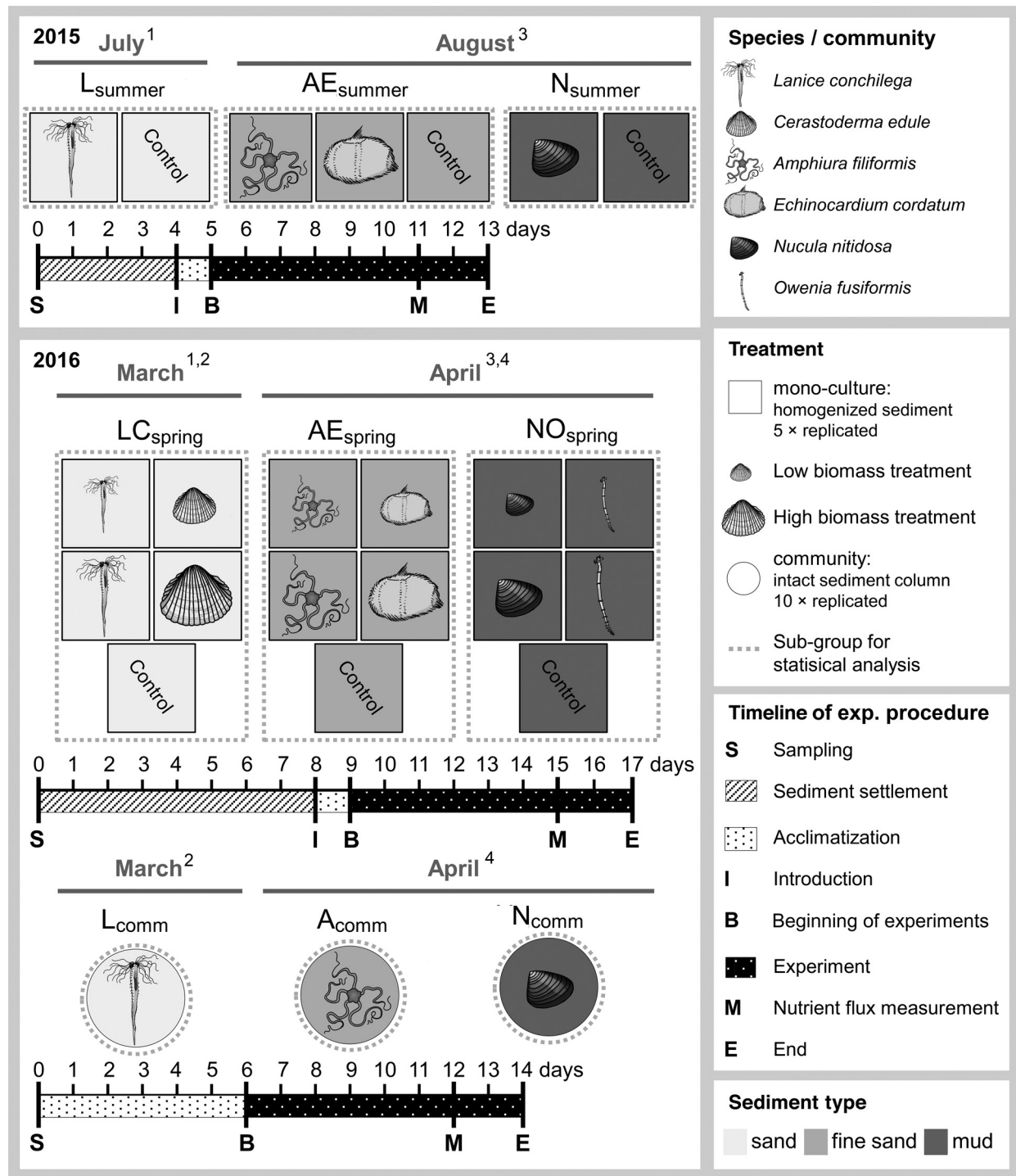


Fig. 1. Summary of experimental procedures and sub-groups for statistical analysis. Monoculture experiments were conducted in rectangular cores, while the community experiments were conducted in cylindrical cores. Sediment settlement in the monoculture experiment was 4 d longer for the spring 2016 experiments than for the summer 2015 experiments. The low and high biomass treatment of the monoculture experiment in spring 2016 differed only in the size of the organisms, not their density. Densities in all monoculture experiments were 5 ind. core⁻¹ for *Lanice conchilega*, *Amphiura filiformis*, *Nucula nitidosa* and *Owenia fusiformis*, 2 ind. core⁻¹ for *Cerastoderma edule* and 1 ind. core⁻¹ for *Echinocardium cordatum*. For the statistical analysis, we summarized the data into 9 sub-groups of homogeneous within-group conditions (i.e. treatment) which are highlighted by the dashed line. The 4 data subsets for which full factorial analyses were carried out are indicated by index numbers 1–4

Table 1. Community bioturbation potential (BP_c) and irrigation potential (IP_c) characteristics of 6 species in the monoculture incubations scored according to Queirós et al. (2013) and Wrede et al. (2017). Mobility: 1, living in fixed tube; 2, limited movement; 3, slow free movement; 4, movement through burrow system. Reworking type: 1, epifauna; 2, surficial modifiers; 3, upward or downward conveyor; 4, biodiffusors. Feeding type: 1, surface filter feeder; 2, predator; 3, deposit feeder; 4, sub-surface filter feeder. Burrow type: 1, epifauna or internal irrigation (i.e. siphons); 2, open irrigation (i.e. Y- or U-shaped burrow); 3, blind ended burrow. Irrigation depth (also termed injection pocket depth by Wrede et al. 2018): 1, 0–2 cm; 2, 2–5 cm; 3, 5–10 cm; 4, >10 cm

Species	BP _c		IP _c		
	Mobility	Reworking type	Feeding type	Burrow type	Irrigation depth
<i>Lanice conchilega</i>	1	3	3	3	3
<i>Cerastoderma edule</i>	2	2	1	1	1
<i>Amphiura filiformis</i>	3	4	4	2	3
<i>Echinocardium cordatum</i>	3	4	3	3	4
<i>Nucula nitidosa</i>	3	2	3	3	1
<i>Owenia fusiformis</i>	1	2	3	3	1

concentrations were similar to the ambient conditions in the Sylt-Rømø Bight (Table 2).

2.3. Measurements of nutrient fluxes and bioirrigation

Nutrient concentrations of nitrite [NO₂⁻], nitrate [NO₃⁻], ammonium [NH₄⁺], silicate [SiO₂] and phosphate [PO₄³⁻] were measured over 8 h on the seventh day after the start of the experiments (Fig. 1). At the start of the incubation (*t*₀), water flow was stopped and a sodium bromide solution was carefully stirred into the water column of each core for assessment of bioirrigation. Aerating each core via an air stone ensured constant oxygen levels in the seawater, similar to *in situ* conditions. Seawater samples of 8 ml (summer 2015) or 13 ml (spring 2016) were extracted and filtered (0.2 µm surfactant-free cellulose acetate membrane; Minisart Syringe Filter, Sartorius) after 0 and 8 h (*t*₀, *t*₈) for the measurement of nutrient concentrations. This time frame and sampling routine was chosen in accordance with Murray et al. (2013), assuming a linear flux over time. A higher sampling frequency, which would have allowed resolving fluctuations and nonlinear fluxes, was rejected due to higher water demand which would have reduced the overlying water column within the cores more strongly. For bioirrigation measurements, further 3 ml samples were taken at *t*₀, *t*₂, *t*₄, *t*₈ and *t*₁₂ (for the summer 2015 experiments only up to *t*₈). The water samples were stored at 3°C until analysis by ion-chromatography (Metrohm, 930 Compact IC Flex). Nutrient samples were divided and stored for the measurement of [SiO₂] at 3°C and for [PO₄³⁻],

[NH₄⁺], [NO₃⁻] and [NO₂⁻] at -20°C. Samples were analysed by segmented flow analyses (SEAL AA3 HR Autoanalyser) and ISO standard procedures (MT 18, MT 19) of the manufacturer (SEAL Analytical) (for detection limits, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m632p027_supp.pdf). Fluxes of [PO₄³⁻], [SiO₂], [NH₄⁺], [NO₃⁻] and [NO₂⁻] in µmol m⁻² h⁻¹ were determined from the changes in concentration over time, multiplied by the overlying water volume and divided by the surface area. Phosphate flux was only measured in spring 2016. Owing to a malfunction of the autoanalyser, the measured nitrate flux values of 33 cores had to be excluded from further analysis.

The bioirrigation activity of the organisms was calculated as described by De Smet et al. (2016):

$$Q = -\frac{V_{ow}}{C_{t_0} - C_{t_{reference}}} \times \frac{dC_{t_0}}{dt} \quad (1)$$

where *Q* is the bioirrigation activity per core (l h⁻¹), *V*_{ow} is the volume of the water overlying the sediment, *C*_{*t*₀} is the bromide (Br⁻) concentration at *t*₀, i.e. directly after adding the bromide tracers to the water column, *C*_{*t*_{reference}} is the ambient Br⁻ concentration of seawater, and *dC*_{*t*₀}/*dt* is the slope of the linear regressions of the Br⁻ concentration versus time over the incubation period. The bioirrigation rate in l m⁻² h⁻¹ was calculated by dividing *Q* by the surface area of the respective cores. In 32 cases, the Br⁻ concentration increased with time (i.e. negative bioirrigation), due to methodological errors or to erroneous first or last measurement; accordingly, these values were excluded (Table S2). Additionally, 1 outlier was removed from the analysis (Table S2).

2.4. Determination of body mass

Organisms that survived the experimental period of 9 d were recovered and fixed in either ethanol (95%) (summer 2015) or in a buffered 5% formaldehyde solution (spring 2016) for subsequent estimation of macrofaunal body mass. After at least 3 mo of storage, species taxonomy was determined. The density was counted, and wet mass (g WM), dry mass (g DM) and ash-free dry mass (g AFDM) of each species per core were measured. In accordance with Wetzel et al. (2005), we assumed that

Table 2. Concentrations (mean \pm SD) of phosphate, silicate, ammonium, nitrate and nitrite in $\mu\text{mol l}^{-1}$ at the start of the incubations. Number of fluxes (n) measured for each of the 9 treatment categories at temperature T ($^{\circ}\text{C}$). $n_{\text{NO}_3^-}$ gives the number of datasets that were included in the statistical assessment of $\Delta[\text{NO}_3^-]$. Blank spaces indicate that no data were available (phosphate) or were excluded due to errors (nitrate). Treatments are illustrated in Fig. 1

Treatment	n	$n_{\text{NO}_3^-}$	T	$[\text{PO}_4^{3-}]$	$[\text{NO}_2^-]$	$[\text{NO}_3^-]$	$[\text{NH}_4^+]$	$[\text{SiO}_2]$
L _{comm}	10	10	8	0.65 ± 0.017	0.38 ± 0.020	39.25 ± 0.237	1.75 ± 0.450	27.86 ± 0.210
LC _{spring}	23	22	8	0.48 ± 0.025	0.28 ± 0.008	38.25 ± 0.351	1.07 ± 0.395	23.08 ± 0.842
L _{summer}	10	10	15		0.55 ± 0.027	3.75 ± 0.113	1.65 ± 0.530	6.32 ± 0.0962
A _{comm}	10	10	8	0.16 ± 0.005	0.16 ± 0.006	15.28 ± 0.549	1.40 ± 0.221	2.58 ± 0.116
AE _{spring}	24	–	8	0.19 ± 0.005	0.18 ± 0.002		2.05 ± 0.127	2.36 ± 0.116
AE _{summer} ^a	18	18	19		0.46 ± 0.015	5.36 ± 0.189	1.69 ± 0.319	8.40 ± 0.361
N _{comm}	10	10	8	0.19 ± 0.013	0.17 ± 0.006	14.02 ± 0.249	2.16 ± 0.284	3.83 ± 0.538
NO _{spring}	25	20	8	0.20 ± 0.003	0.19 ± 0.003	12.30 ± 0.141	2.02 ± 0.123	2.30 ± 0.207
N _{summer} ^a	10	10	19		0.43 ± 0.009	5.55 ± 0.088	1.59 ± 0.288	8.33 ± 0.323

^aData taken from Wrede et al. (2017)

there are no significant differences in the body mass measurements between alcohol- or formaldehyde-fixed samples. Density and biomass values were standardized to ind. m^{-2} or g m^{-2} .

2.5. Calculation of bioturbation and irrigation potential

The irrigation potential (IP) of the community in each core (IP_c) was calculated according to Wrede et al. (2018) by:

$$\text{IP}_c = \sum_{i=1}^n \left(\frac{B_i}{A_i} \right)^{0.75} \times A_i \times BT_i \times FT_i \times ID_i \quad (2)$$

where A_i and B_i are density and biomass of species i , and BT_i , FT_i and ID_i are categorical scores describing burrow type, feeding type and irrigation depth (also termed injection pocket depth by Wrede et al. 2018). Categorical scores on irrigation traits were compiled from the classifications provided by Wrede et al. (2018) (Table 1).

The bioturbation potential (BP) of the community in each core (BP_c) was calculated according to Solan et al. (2004) and Queirós et al. (2013):

$$\text{BP}_c = \sum_{i=1}^n \left(\frac{B_i}{A_i} \right)^{0.5} \times A_i \times M_i \times R_i \quad (3)$$

where A_i and B_i are density and biomass of species i at a station, and M_i and R_i are categorical scores describing the mobility and reworking mode of species i , respectively. Categorical scores were adopted from the classifications provided by Queirós et al. (2013). Missing information on mobility and reworking modes was compiled from literature following the rules proposed by Queirós et al. (2013).

In order to assess whether irrigation traits or the body mass scaling factor are responsible for differences between IP_c and BP_c , we also calculated a modified IP_c (mIP_c). To do so, we replaced the IP_c body mass scaling factor of 0.75 with the BP_c body mass scaling factor of 0.5. Both IP_c and BP_c , as well as mIP_c , were calculated based on both WM and AFDM.

All community descriptors were calculated per m^2 . The controls of the monoculture experiments were included in all analyses with IP_c , mIP_c and $\text{BP}_c = 0$.

2.6. Statistical analysis

In total, data on nitrite, ammonium and silicate fluxes were available for 140 individually assessed cores, while there were 110 for nitrate and 102 for phosphate (Fig. 1, Table 2). These numbers include the controls of the monoculture experiments. Due to time and space limitations, experiments with the different sediment types were conducted in different months (i.e. sand was measured in March and July; fine sand and mud were measured in April and August). As the experimental water was provided by a constant flow source from the Sylt-Rømø Bight, initial nutrient concentrations in the water column differed between experiments with respect to the time point of the experiments (Table 2). Hence, full factorial analysis was not possible for the whole dataset. Still, in 4 different subsets of the data, sediment and time point of the experiment were independent and they could be analysed as full factorial experiments (Fig. 1). We conducted both the analysis of the 4 full factorial subsets and an analysis of the whole data set. As the whole data set provides more insight into how the community predictors function under condi-

tions faced by possible users, i.e. heterogeneity in data is the reality of many macrozoobenthos datasets, we emphasize the findings of the analysis of the whole data set.

For the whole data set, to test whether different environmental conditions affect the capability of IP_c or BP_c in predicting nutrient fluxes in general, the experimental units (cores) were assigned to 9 different treatments (Fig. 1, Table 2). Within each category of the variable 'treatment', the cores received the same sediment type, sediment manipulation (sieved homogenized sediment of monocultures vs. *in situ* stratification of communities) and seawater of the same initial nutrient concentration and temperature. Previous studies have shown that these parameters can particularly affect nutrient fluxes (Mermillod-Blondin & Rosenberg 2006, Baranov et al. 2016, Biswas et al. 2017). Within treatments, community descriptors varied through varying faunal composition. For the 4 full factorial data subsets, we used the factors season (spring, summer), sediment type (fine sand, mud) and manipulation (single-species, multi-species) where applicable, together with the community descriptors.

To describe the relationship between nutrient flux and community parameters or trait-based indices for the whole data set, we constructed generalized linear models (GLMs) of nitrite, nitrate, ammonium, silicate and phosphate fluxes as a function of community descriptors x (i.e. Density, WM, AFDM, $IP_{c,WM}$, $IP_{c,AFDM}$, $mIP_{c,WM}$, $mIP_{c,AFDM}$, $BP_{c,WM}$ or $BP_{c,AFDM}$) the categorical variable 'treatment' (L_{comm} , LC_{spring} , L_{summer} , A_{comm} , AE_{spring} , AE_{summer} , N_{comm} , NO_{spring} , N_{summer} ; see Fig. 1) and the interaction between community descriptors and treatment:

$$\text{Nutrient flux} \sim x + \text{treatment} + \text{interaction}(x:\text{treatment}) \quad (4)$$

Further, individual GLMs of nitrite, nitrate, ammonium, silicate and phosphate flux were constructed for each of the full factorial subsets with a function of the community descriptors x , the environmental factors that were appropriate for the respective subset and the interaction between x and the respective environmental conditions.

To identify the model which best describes the fluxes of each nutrient, we used comparisons of Akaike's information criterion (AIC). The lowest AIC indicates the model closest to full reality in the investigated model set, i.e. the best model in the sense of trading-off bias versus variance of the fitted model parameters, for a given sample size (Zuur et al. 2007, Burnham et al. 2011).

To test if the 3 variables (x , treatment, interaction between treatment and x) are significantly linked to nutrient flux, we applied a subsequent Wald chi-squared test on the best generalized models of each community descriptor.

Calculation of variance inflation factors (VIFs) according to Zuur et al. (2010) demonstrated that there was no collinearity of the community predictors and the treatment or the environmental factors (Table S3). In accordance with Zuur et al. (2010), we chose a very stringent approach where a VIF value >3 was chosen as the threshold for collinearity that was too strong. The different community predictors are naturally collinear among each other but were not applied together within a GLM, because the aim was to compare between them. Visual inspection of the residual plots of the best models did not indicate deviation from homoscedasticity, but from normality for the GLMs of phosphate, silicate, ammonium and nitrite fluxes. Transformation of the data did not achieve normality. According to Quinn & Keough (2002) normality is an important but not a crucial assumption, whereas Gelman & Hill (2007) did not even recommend the diagnostics of normality for GLMs. Yet to reduce the likelihood of a type I error due to non-normality of the data, we lowered the significance level for the Wald chi-squared test to $\alpha < 0.01$.

All analyses were carried out within the R statistical and programming environment (R Core Team 2013). Wald chi-squared analysis of GLMs was performed with the package 'car' (Fox & Weisberg 2011).

3. RESULTS

Absolute fluxes of nitrite, nitrate, ammonium and phosphate were on average largest for L_{comm} (see Fig. 1 for treatment details), whereas the absolute flux of silicate was on average highest in AE_{summer} (Fig. 2). Bioirrigation was on average strongest in AE_{summer} (Fig. 2). Generally, bromide measurements indicated constant irrigation over time for all treatment categories. Densities were highest in the 3 community treatments. The communities were dominated by *Lanice conchilega* for L_{comm} (58% of total density), by *Amphiura filiformis* (62% of total density) for A_{comm} and *Owenia fusiformis* (31% of total density) and *Nucula nitidosa* (26% of total density) for N_{comm} (for a detailed species list including trait scores, see Table S4).

Average biomass (i.e. WM and AFDM) was highest in LC_{spring} due to the *Cerastoderma edule* cores (Fig. 3). In combination with the sediment reworking

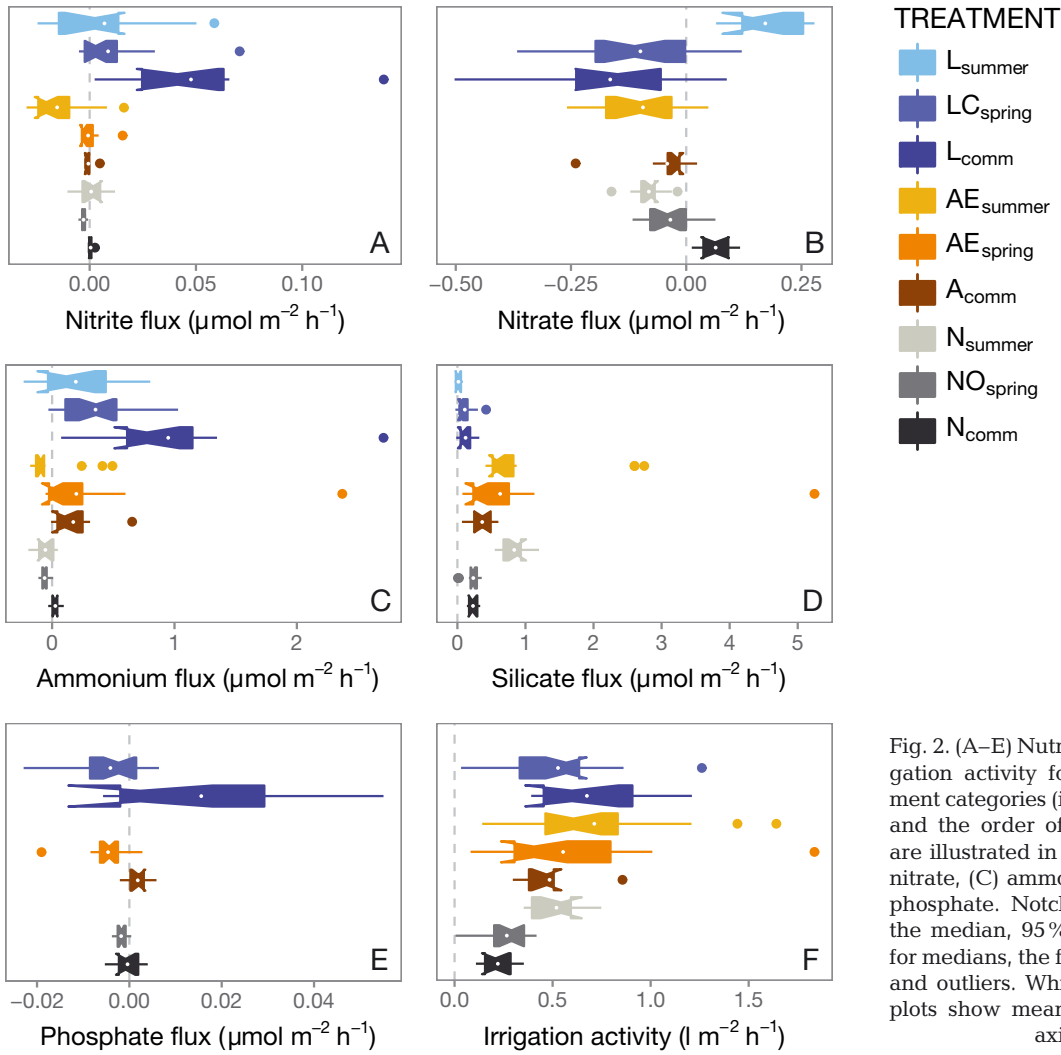


Fig. 2. (A–E) Nutrient fluxes and (F) irrigation activity for the different treatment categories (indicated by the colour and the order of the bars; treatments are illustrated in Fig. 1): (A) nitrite, (B) nitrate, (C) ammonium, (D) silicate, (E) phosphate. Notched boxplots indicate the median, 95 % confidence intervals for medians, the first and third quartiles and outliers. White points on the boxplots show means. Note the different axis scales

traits of *C. edule* (Table 1), average BP_c of $\text{LC}_{\text{spring}}$ was higher (30 % for $\text{BP}_{c,\text{WM}}$, 7 % for $\text{BP}_{c,\text{AFDM}}$) than average BP_c of L_{comm} (Fig. 3). The absolute fluxes (i.e. independent of direction) of all nutrients as well as the bioirrigation activity were on average stronger in the L_{comm} cores (i.e. 449 % for nitrite, 65 % for nitrate, 167 % for ammonium, 10 % for silicate, 227 % for phosphate and 70 % for the irrigation activity) (Fig. 2). Similarly, the values of the irrigation trait-based indices (i.e. $\text{IP}_{c,\text{WM}}$, $\text{IP}_{c,\text{AFDM}}$, $\text{IP}_{c,\text{WM}}$, $\text{IP}_{c,\text{AFDM}}$) were on average more than 2 times higher for L_{comm} than for L_{spring} (Fig. 3). Furthermore, there were strong differences in the magnitude of $\text{AE}_{\text{spring}}$ and A_{comm} between the indices and body mass units. Values of all indices were on average lower for $\text{AE}_{\text{spring}}$ than for A_{comm} (in the order of magnitude: $\text{BP}_{c,\text{AFDM}}$ 119 %, $\text{mIP}_{c,\text{AFDM}}$ 75 %, $\text{BP}_{c,\text{WM}}$ 60 %, $\text{mIP}_{c,\text{WM}}$ 27 %, $\text{IP}_{c,\text{AFDM}}$ 14 %), with only $\text{IP}_{c,\text{WM}}$ as the exception having on average one-third higher values for $\text{AE}_{\text{spring}}$ (Fig. 3).

The latter corresponds to the stronger average absolute fluxes (i.e. independent of direction) of nitrite (6 %), ammonium (12 %), silicate (42 %) and phosphate (60 %) as well as higher average irrigation activity (17 %) in $\text{AE}_{\text{spring}}$ compared to A_{comm} (Fig. 2).

For the whole data set nitrite, nitrate, ammonium and silicate fluxes across the sediment–water interface were best (i.e. lowest AIC) described with a function of $\text{IP}_{c,\text{WM}}$, treatment and the interaction between treatment and $\text{IP}_{c,\text{WM}}$ (for detailed coefficient tables of the best models, see Tables S5–S9). In contrast, phosphate flux was best (i.e. lowest AIC) predicted by a function of $\text{mIP}_{c,\text{AFDM}}$ and treatment (Table 3).

All fluxes across the sediment–water interface were significantly ($\alpha < 0.01$; Table 4) associated with the irrigation potential, irrespective of the body mass unit (i.e. $\text{IP}_{c,\text{AFDM}}$ or $\text{IP}_{c,\text{WM}}$). Treatment affected the rates of all measured fluxes signifi-

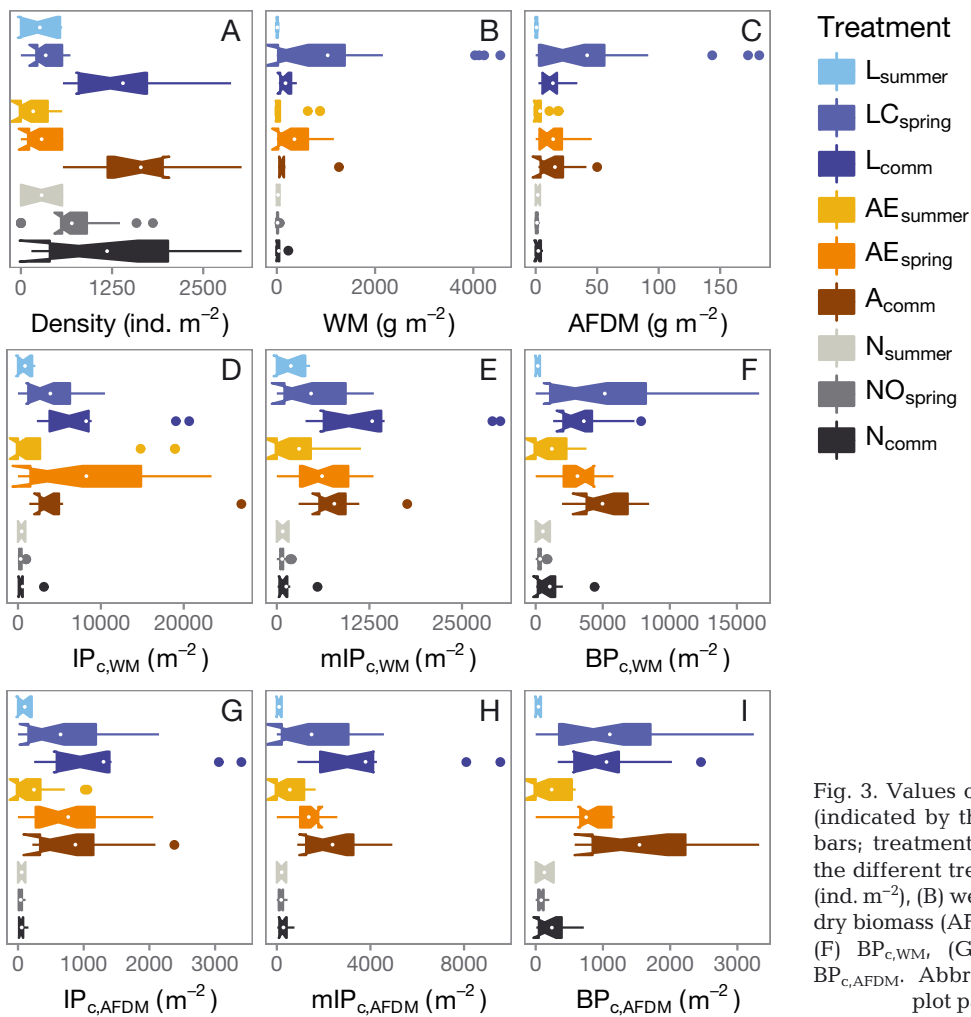


Fig. 3. Values of the 9 community descriptors (indicated by the colour and the order of the bars; treatments are illustrated in Fig. 1) for the different treatment categories: (A) density (ind. m⁻²), (B) wet biomass (WM; g), (C) ash-free dry biomass (AFDM; g), (D) IP_{c,WM}, (E) mIP_{c,WM}, (F) BP_{c,WM}, (G) IP_{c,AFDM}, (H) mIP_{c,AFDM}, (I) BP_{c,AFDM}. Abbreviations as in Table 3; box plot parameters as in Fig. 2

cantly ($\alpha < 0.01$; Table 4). A significant interaction of IP_c, irrespective of the body mass unit (i.e. IP_{c,AFDM} or IP_{c,WM}), and treatment was found for nitrite, nitrate and silicate fluxes (for the results of BP_c and the other community descriptors, see Table S10).

Nitrite flux and IP_{c,WM} were positively related except for A_{comm} and NO_{spring} (Fig. 4). Nitrate flux was negatively linked to IP_{c,WM} for all treatment categories (Fig. 5). Ammonium flux and IP_{c,WM} were positively associated except for A_{comm} and AE_{summer} (Fig. 6), whereas the relationship between silicate flux and IP_{c,WM} was negative except for AE_{spring} and NO_{spring} (Fig. 7). The relationship between phosphate flux and mIP_{c,AFDM} was positive (Fig. 8).

Models containing irrigation trait-based indices (i.e. IP_c or mIP_c) generally had lower AIC values (see Table 3) than models including density, biomass or BP_c (Table 3). Likewise, irrigation trait-

based indices were included in all but one of the best models of the 4 different full factorial analyses (Table 5; for full AIC tables, see Tables S11–S14). In 6 cases out of 16, the best model contained the index alone (Table 5). In the full factorial analyses, significant interactions were only detected between index and season or sediment and season, apart from one exception where phosphate flux in April 2016 (data subset 4) was best predicted as a function of AFDM, sediment, manipulation and interactions between all variables.

In the whole data set, models describing nutrient fluxes as a function of the community descriptor alone (i.e. nutrient flux ~ x) mostly performed less well (i.e. higher AIC values) than models describing nutrient fluxes as a function of treatment (i.e. nutrient flux ~ treatment) (Table 3). This general pattern was not true for ammonium flux, where a function of IP_{c,AFDM}, mIP_{c,AFDM} or mIP_{c,WM} had a lower AIC than a function of treatment alone.

4. DISCUSSION

Our findings clearly demonstrate that the IP_c as proposed by Wrede et al. (2018) is a suitable, but not sufficient, predictor of nutrient fluxes across the sediment–water interface. Different environments already vary intrinsically in their nutrient fluxes (Mermillod-Blondin & Rosenberg 2006, Baranov et al. 2016, Biswas et al. 2017), as biogeochemical cycling is also a function of many other ecosystem characteristics such as total organic content, permeability, temperature, gradients across the sediment–water interface, currents and turbulence (Krantzberg 1985, Huettel & Gust 1992, Mermillod-Blondin & Rosenberg 2006, Wohlge-muth et al. 2017). Hence organisms with similar traits affect nutrient fluxes differently in different ecosystems (Mermillod-Blondin & Rosenberg 2006). Accordingly, the categorical variable ‘treatment’, which accounts for the different environmental conditions in our whole dataset analysis, significantly affects all analysed nutrient fluxes and interacts with IP_c for nitrate, nitrite, ammonium and silicate. This is in contrast to the full factorial analyses where, except for phosphate, the only interactions were found with the variable season. With this additional knowledge, the interaction of index with treatment in the full data set is likely to be ascribed to an interaction of index with season, while the effect of sediment is additive. This is not surprising, as not only does the activity of coastal benthic macrofauna change with temperature and season (Grant 1986, Thamdrup et al. 1998, Provoost et al. 2013), but coastal sediment biogeochemistry and resulting nutrient fluxes are also strongly modulated by seasonal variation in temperature, organic matter input and gradients across the sediment–water interface (Provoost et al. 2013, Braeckman et al. 2014). Quantitative predictions of nutrient fluxes based on the macrofaunal traits alone will thus be difficult to realize, especially in temporally heterogeneous data sets.

Table 3. Akaike’s information criterion (AIC) values of the generalized linear models used to describe phosphate, nitrite, nitrate, ammonium and silicate fluxes as a function of community descriptor (x), treatment (tr) and the interaction (in) between x and tr . The gray scale sets the AIC value in relation to all other models of that particular nutrient flux: the lighter the gray, the lower the AIC and the better the model (note the negative values). Asterisks indicate the best model for the respective community descriptor (x). **Bold** indicates the model and respective community descriptor which have the lowest AIC for the respective nutrient flux. AFDM: ash-free dry mass; WM: wet mass; IP_c : community irrigation potential; mIP_c : modified IP_c ; BP_c : community bioturbation potential

Nutrient	AIC for the different degrees of model complexity					x
	~ 1	$\sim tr$	$\sim x$	$\sim x + tr$	$\sim x + tr + in$	
Phosphate	-653	-685*	-662	-683	-683	Density
	-653	-685	-654	-685	-689*	AFDM
	-653	-685	-657	-686	-688*	WM
	-653	-685	-668	-696*	-693	$IP_{c,AFDM}$
	-653	-685	-657	-689	-694*	$IP_{c,WM}$
	-653	-685	-680	-699*	-692	$mIP_{c,AFDM}$
	-653	-685	-677	-697*	-695	$mIP_{c,WM}$
	-653	-685*	-651	-683	-683	$BP_{c,AFDM}$
	-653	-685	-651	-683	-686*	$BP_{c,WM}$
	-692	-767	-703	-769	-775*	Density
Nitrite	-692	-767	-692	-765	-788*	AFDM
	-692	-767	-690	-765	-785*	WM
	-692	-767	-741	-806	-821*	$IP_{c,AFDM}$
	-692	-767	-713	-794	-829*	$IP_{c,WM}$
	-692	-767	-758	-810	-813*	$mIP_{c,AFDM}$
	-692	-767	-758	-820	-825*	$mIP_{c,WM}$
	-692	-767	-701	-768	-781*	$BP_{c,AFDM}$
	-692	-767	-696	-767	-783*	$BP_{c,WM}$
	-135	-190	-137	-198	-201*	Density
	-135	-190	-144	-196	-216*	AFDM
Nitrate	-135	-190	-139	-191	-208*	WM
	-135	-190	-165	-217	-235*	$IP_{c,AFDM}$
	-135	-190	-148	-195	-247*	$IP_{c,WM}$
	-135	-190	-169	-221	-225*	$mIP_{c,AFDM}$
	-135	-190	-160	-212	-233*	$mIP_{c,WM}$
	-135	-190	-156	-212	-219*	$BP_{c,AFDM}$
	-135	-190	-151	-201	-220*	$BP_{c,WM}$
	155	98*	150	99	99	Density
	155	98	134	85	66*	AFDM
	155	98	141	87	62*	WM
Ammonium	155	98	81	54*	61	$IP_{c,AFDM}$
	155	98	99	45	40*	$IP_{c,WM}$
	155	98	84	68*	75	$mIP_{c,AFDM}$
	155	98	64	44*	56	$mIP_{c,WM}$
	155	98	121	82*	84	$BP_{c,AFDM}$
	155	98	122	79	68*	$BP_{c,WM}$
	258	229*	257	231	238	Density
	258	229	260	229	184*	AFDM
	258	229	259	227	174*	WM
	258	229	255	216	183*	$IP_{c,AFDM}$
Silicate	258	229	230	186	169*	$IP_{c,WM}$
	258	229	259	224	206*	$mIP_{c,AFDM}$
	258	229	253	207	176*	$mIP_{c,WM}$
	258	229	260	228	228*	$BP_{c,AFDM}$
	258	229	259	225	194*	$BP_{c,WM}$

Additionally, both IP_c and BP_c are not suited to predict nutrient fluxes in very permeable, very deeply oxygenized systems (e.g. gravel, maerl), as in these

Table 4. Results of the Wald chi-squared test of the best (lowest AIC) generalized linear models of nitrite, nitrate, ammonium, silicate and phosphate as a function of the community descriptor (x) (irrigation potential [IP_c] based on wet mass [WM] or on ash-free dry mass [AFDM]), the treatment (tr) and the interaction (in) between x and tr . Dashes indicate that the interaction was not included in the lowest AIC model. Blanks indicate that there was no significant impact of the variable. Asterisks indicate significance at $\alpha < 0.01$

x	Nutrient	χ^2			df			$p > \chi^2$		
		x	tr	in	x	tr	in	x	tr	in
$IP_{c,AFDM}$	Nitrite	52.14	119.67	30.24	1	8	8	*	*	*
	Nitrate	37.74	103.23	31.94	1	7	7	*	*	*
	Ammonium	51.12	46.59	—	1	8	—	*	*	—
	Silicate	19.23	83.56	51.45	1	8	8	*	*	*
	Phosphate	12.96	42.75	—	1	5	—	*	*	—
$IP_{c,WM}$	Nitrite	40.27	174.10	52.93	1	8	8	*	*	*
	Nitrate	10.87	128.77	78.54	1	7	7	*	*	*
	Ammonium	68.98	91.87	19.52	1	8	8	*	*	*
	Silicate	57.21	82.72	32.90	1	8	8	*	*	*
	Phosphate	6.84	53.23	14.52	1	5	5	*	*	*

systems, macrofaunal impact on nutrient fluxes is very limited (Huettel & Webster 2001). However, within appropriate settings (e.g. mud, fine sand, sand), IP_c can be a valuable tool to complement BP_c .

While a function of treatment alone (i.e. flux $\sim tr$) described nutrient fluxes across the sediment–water interface in most cases better than a function of IP_c — or any of the other tested community descriptors — alone (i.e. flux $\sim x$), models containing both the IP_c and treatment (or environmental conditions for the full factorial analyses) with and without an interaction were always better than functions of the latter alone. Hence, linking bioirrigation activity to important environmental factors should, in accordance with the general consensus in early diagenetic modelling (Boulton et al. 2002, Mermillod-Blondin & Rosenberg 2006, Meysman et al. 2006), enhance ecosystem models of nutrient fluxes distinctly, especially as an irrigation-trait based index was a significant variable in all but one of the best models.

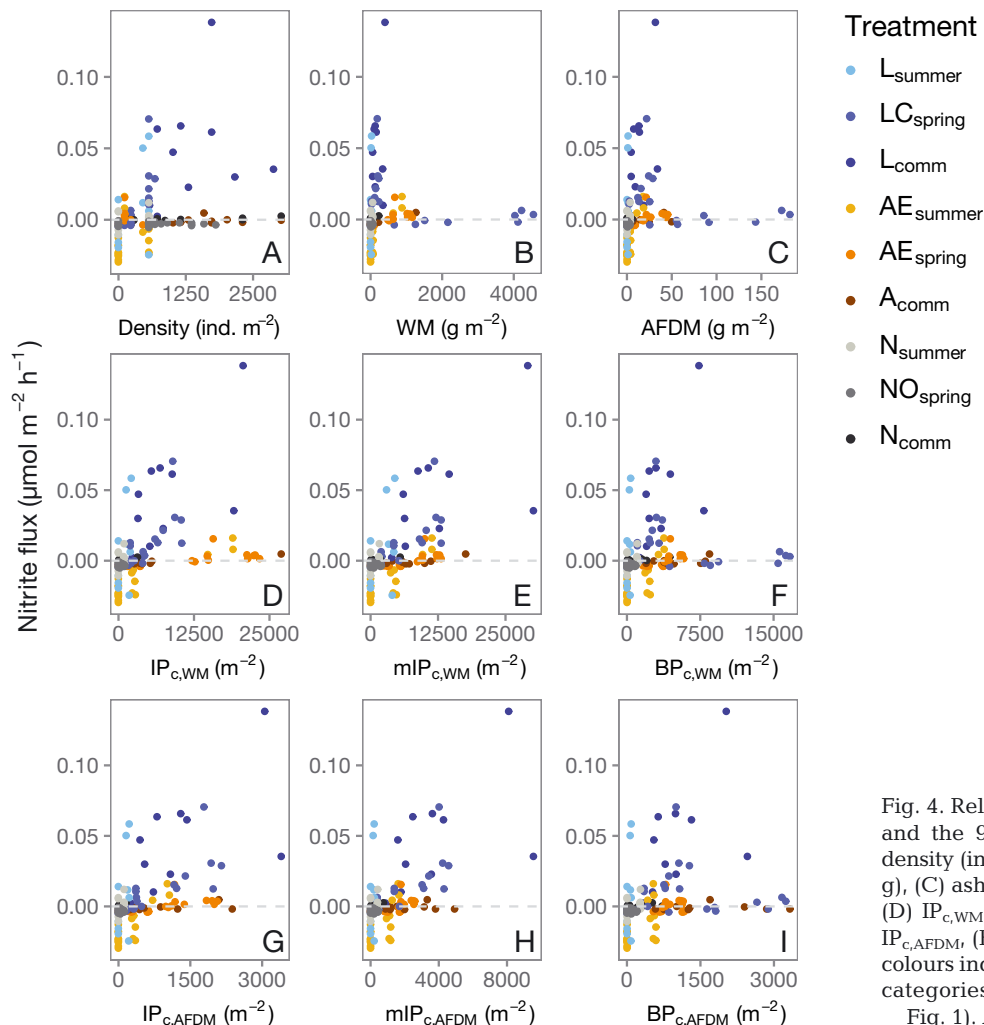


Fig. 4. Relationship between nitrite flux and the 9 community descriptors: (A) density (ind. m^{-2}), (B) wet biomass (WM; g), (C) ash-free dry biomass (AFDM; g), (D) $IP_{c,WM}$, (E) $mIP_{c,WM}$, (F) $BP_{c,WM}$, (G) $IP_{c,AFDM}$, (H) $mIP_{c,AFDM}$, (I) $BP_{c,AFDM}$. The colours indicate the different treatment categories (treatments are illustrated in Fig. 1). Abbreviations as in Table 3

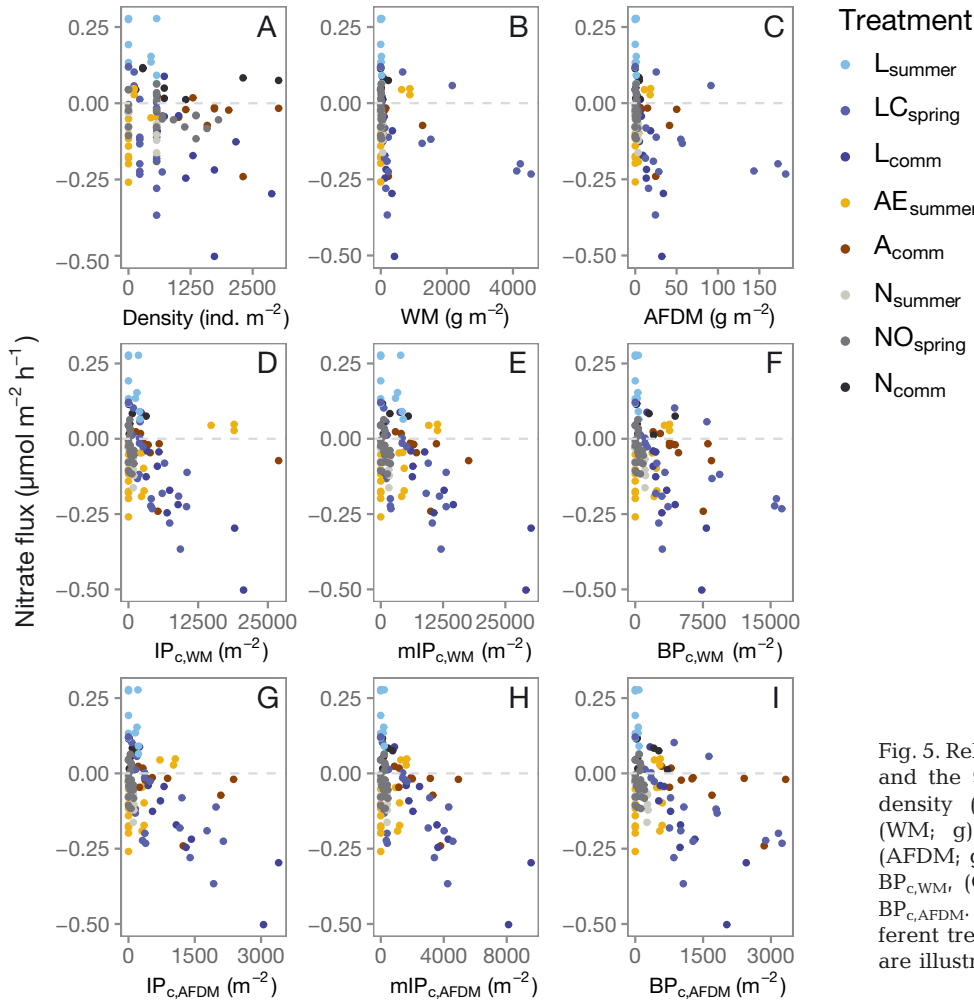


Fig. 5. Relationship between nitrate flux and the 9 community descriptors: (A) density (ind. m^{-2}), (B) wet biomass (WM; g m^{-2}), (C) ash-free dry biomass (AFDM; g m^{-2}), (D) $\text{IP}_{\text{c,WM}}$, (E) $\text{mIP}_{\text{c,WM}}$, (F) $\text{BP}_{\text{c,WM}}$, (G) $\text{IP}_{\text{c,AFDM}}$, (H) $\text{mIP}_{\text{c,AFDM}}$, (I) $\text{BP}_{\text{c,AFDM}}$. The colours indicate the different treatment categories (treatments are illustrated in Fig. 1). Abbreviations as in Table 3

In nearly all cases, models containing mIP_{c} had lower AIC values than models containing density, biomass or BP_{c} . This was both the case for models with interaction and without interaction. Consequently, the merit of IP_{c} in complementing BP_{c} is a direct result of the description of macrofaunal activity via irrigation traits, and not only caused by the different body mass scaling factors between IP_{c} and BP_{c} . The ability of the different indices to predict the nutrient fluxes in L_{comm} and $\text{LC}_{\text{spring}}$ provides a good example for the effects of the different traits. While the sediment reworking traits in BP_{c} weight the activity of *Lanice conchilega* and *Cerastoderma edule* similarly, the irrigation traits in IP_{c} or mIP_{c} weight the activity of *L. conchilega* 3 times higher than that of *C. edule*. This is in accordance with the higher bioirrigation activity and the higher nitrite, nitrate, ammonium, silicate and phosphate fluxes and of L_{comm} .

Some differences between BP_{c} and IP_{c} were also caused by the scaling factor. A scaling factor of 0.5,

as used in BP_{c} or mIP_{c} , puts more weight on species with low body mass and with high density (i.e. in our experiments primarily *Amphiura filiformis* in A_{comm}), while the scaling factor of 0.75, as used in IP_{c} , puts more weight on large organisms even if they are not abundant (i.e. in our experiments mainly *Echinocardium cordatum* in $\text{AE}_{\text{spring}}$). Thus, mIP_{c} had higher values for A_{comm} on average, whereas $\text{IP}_{\text{c,WM}}$ showed higher average values for $\text{AE}_{\text{spring}}$. The plausibility of the latter is endorsed by the higher nitrite, ammonium and silicate fluxes as well as higher average irrigation activity in $\text{AE}_{\text{spring}}$. Consequently, an exponent of 0.75 may account better for the scaling of metabolic activity with body mass (West & Brown 2005, Brey 2010), thereby enhancing the predictability of nutrient fluxes.

While IP_{c} profits from its irrigation traits and in specific cases from the scaling factor, it is more difficult to discern which body mass unit should be used in its application. Contrary to our second hypothesis, per-

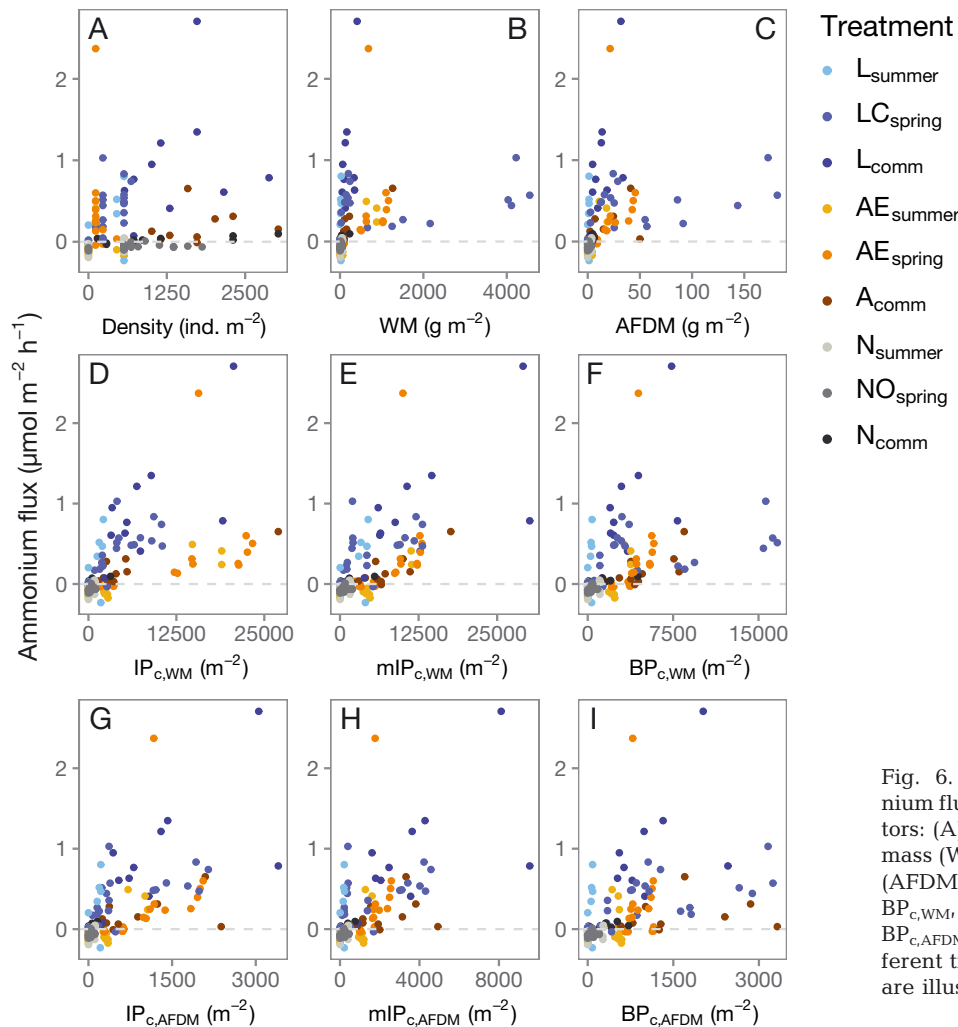


Fig. 6. Relationship between ammonium flux and the 9 community descriptors: (A) density (ind. m^{-2}), (B) wet biomass (WM; g), (C) ash-free dry biomass (AFDM; g), (D) $IP_{c,WM}$, (E) $mIP_{c,WM}$, (F) $BP_{c,WM}$, (G) $IP_{c,AFDM}$, (H) $mIP_{c,AFDM}$, (I) $BP_{c,AFDM}$. The colours indicate the different treatment categories (treatments are illustrated in Fig. 1). Abbreviations as in Table 3

formance of IP_c as a predictor of nutrient fluxes was mostly better when based on WM instead of AFDM. AFDM represents the biologically active part of an organism and is therefore a reasonable proxy of metabolic activity, whereas WM (including fluid and inorganic parts) may be a better proxy of body volume. Organism size and volume are critically linked with the scope of macrofaunal sediment interactions as well as burrow size and burrow wall area (Bender & Davis 1984, Wheatcroft et al. 1990, Twitchett 1999), which in turn are crucial determinants of nitrogen cycling and nutrient fluxes (Aller 1988, Laverock et al. 2011). While the ratio of AFDM and WM does not vary much across many taxa, it can be extremely low in taxa with exoskeletons. Accordingly, some of these species, such as the sea urchin *E. cordatum*, which may strongly enhance nutrient fluxes and biogeochemical cycling (Lohrer et al. 2004, Wrede et al. 2017), are dramatically underrepresented if they are described via AFDM. This may explain why the use

of WM as the body mass unit in $IP_{c,WM}$ leads to better predictions of nitrite, nitrate and ammonium fluxes than the use of AFDM in $IP_{c,AFDM}$.

Phosphate behaves differently. In our whole dataset analysis, we observed a positive link between phosphate flux and $mIP_{c,AFDM}$, which indicates either reduced inflow of phosphate into the sediment or increased outflow of phosphate into the water column at increasing irrigation. Macrofaunal activity may enhance phosphate release from sediments as a result of excretion or egestion (Gallepp 1979, Gardner et al. 1981, Krantzberg 1985, Dupont et al. 2006) or by rapid intensive advective flushing of anoxic sediment layers (Carlton & Wetzel 1988, Biswas et al. 2017). As phosphate release in the whole dataset analysis scales better with $mIP_{c,AFDM}$ (i.e. a proxy for the metabolic activity of the inhabiting fauna) than with $IP_{c,WM}$ or $mIP_{c,WM}$ (i.e. a proxy for the volume of the organism), one might conclude that the positive correlation between $IP_{c,AFDM}$ and phosphate in our

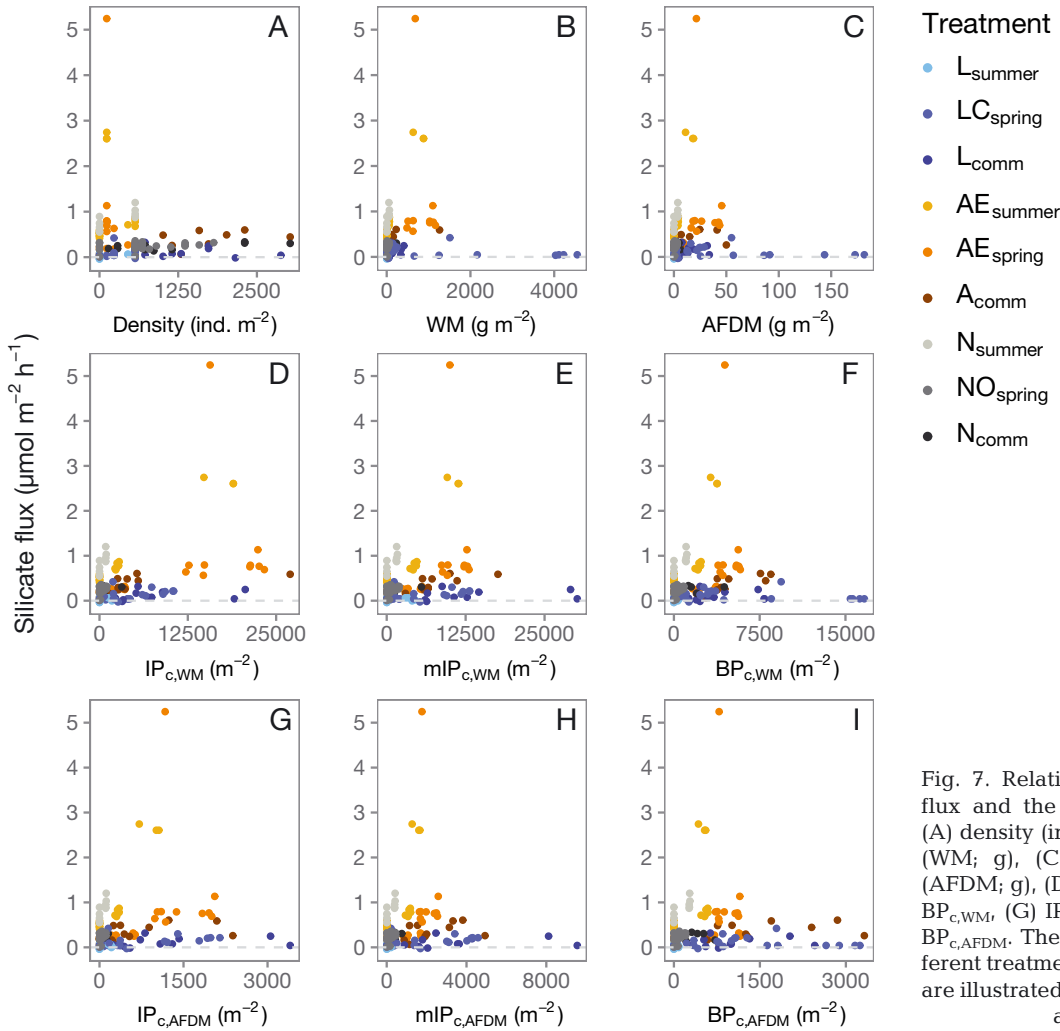


Fig. 7. Relationship between silicate flux and the community descriptors: (A) density (ind. m^{-2}), (B) wet biomass (WM; g), (C) ash-free dry biomass (AFDM; g), (D) $\text{IP}_{\text{c,WM}}$, (E) $\text{mIP}_{\text{c,WM}}$, (F) $\text{BP}_{\text{c,WM}}$, (G) $\text{IP}_{\text{c,AFDM}}$, (H) $\text{mIP}_{\text{c,AFDM}}$, (I) $\text{BP}_{\text{c,AFDM}}$. The colours indicate the different treatment categories (treatments are illustrated in Fig. 1). Abbreviations as in Table 3

experiments was the result of excretion. However, results from the full factorial analysis are inconsistent. Different processes may be acting in the different treatments.

Ammonium may also be a product of excretion (Henriksen et al. 1983). Yet ammonium flux was clearly predicted best by $\text{IP}_{\text{c,WM}}$, indicating that irrigation and metabolic activity of the macrofaunal organisms alone are not sufficient to describe ammonium flux. Next to excretion, ammonium is a product of aerobic and anaerobic remineralisation within natural sediments (Kristensen 1985, Aller 1988, Laverock et al. 2011). Irrigation may supply oxidants that increase remineralisation and ammonium production (Aller 1988). Irrigation may also stimulate ammonium production in the sediment away from the burrow walls by 20–30% as it removes metabolites that inhibit ammonification (Aller 1988). Moreover, both processes are critically linked to the physical contact between sediment and irrigation flux, explaining

why the irrigated volume might play a crucial role in the cycling of ammonium. However, as we lack data on sediment biogeochemistry and have not measured the irrigated sediment volume, this can only remain a speculation.

In conclusion, IP_{c} is a suitable, and in the case of our study a superior, predictor of nutrient fluxes across the sediment–water interface. The merit of IP_{c} is foremost due to its irrigation traits. IP_{c} thus constitutes a valuable complement to the description of macrofaunal sediment reworking activity by BP_{c} . In addition, the scaling factor of IP_{c} (i.e. 0.75) adds to IP_{c} performance if large organisms, with low densities, are among the faunal inventory. The use of the correct body mass measurement is a further critical determinant of the ability of IP_{c} to predict nutrient fluxes. Indices based on WM provided better predictions of nitrite, nitrate and ammonium than AFDM, as WM may have acted as a proxy of irrigated sediment volume or burrow wall area. While the latter theory still

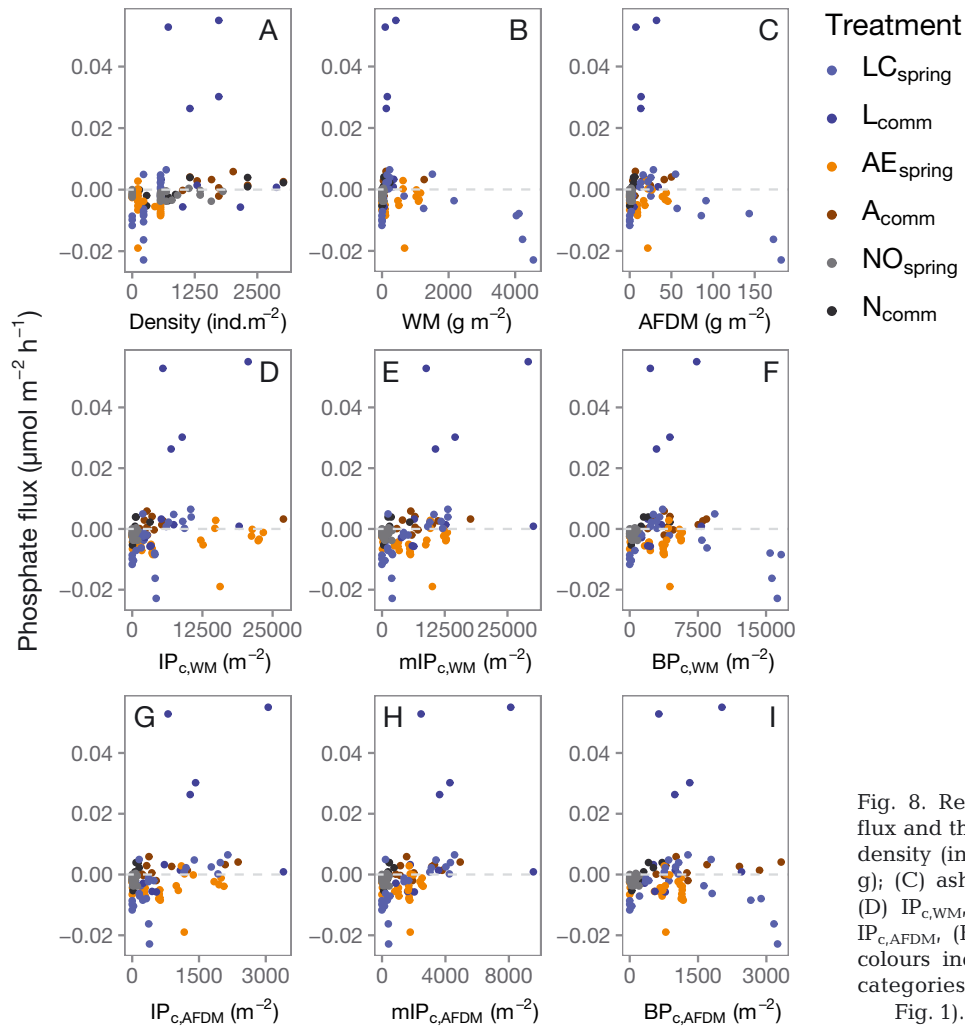


Fig. 8. Relationship between phosphate flux and the 9 community descriptors: (A) density (ind. m⁻²); (B) wet biomass (WM; g); (C) ash-free dry biomass (AFDM; g); (D) IP_{c,WM}, (E) mIP_{c,WM}, (F) BP_{c,WM}, (G) IP_{c,AFDM}, (H) mIP_{c,AFDM}, (I) BP_{c,AFDM}. The colours indicate the different treatment categories (treatments are illustrated in Fig. 1). Abbreviations as in Table 3

Table 5. Best (lowest AIC) generalized linear models of nitrite, nitrate, ammonium, silicate and phosphate fluxes (see Tables S11–S14 for AIC values). Colons (:) indicate interactions, whereas plus signs (+) indicate additive effects. Blanks indicate that no analysis could be performed as data was lacking for a full factorial analysis (see Table 2). Abbreviations as in Table 3; treatments are illustrated in Fig. 1

Data subset	Included treatments	Nutrient	Best model
1	L _{summer} LC _{spring}	Nitrite	Nutrient flux ~ mIP _{c,WM}
		Nitrate	Nutrient flux ~ IP _{c,WM} + Season
		Ammonium	Nutrient flux ~ IP _{c,WM} + Season + IP _{c,WM} :Season
		Silicate	Nutrient flux ~ IP _{c,AFDM} + Season
		Phosphate	
2	L _{comm} LC _{spring}	Nitrite	Nutrient flux ~ IP _{c,WM} + Manipulation
		Nitrate	Nutrient flux ~ IP _{c,WM}
		Ammonium	Nutrient flux ~ IP _{c,WM} + Manipulation
		Silicate	Nutrient flux ~ IP _{c,AFDM}
		Phosphate	Nutrient flux ~ mIP _{c,WM} + Manipulation
3	AE _{summer} AE _{spring} N _{summer} NO _{spring}	Nitrite	Nutrient flux ~ IP _{c,WM} + Season + IP _{c,WM} :Season
		Nitrate	
		Ammonium	Nutrient flux ~ IP _{c,WM}
		Silicate	Nutrient flux ~ IP _{c,WM} + Season + IP _{c,WM} :Season
		Phosphate	
4	A _{comm} AE _{spring} N _{comm} NO _{spring}	Nitrite	Nutrient flux ~ IP _{c,WM} + Manipulation + Sediment + Manipulation:Sediment
		Nitrate	
		Ammonium	Nutrient flux ~ IP _{c,WM}
		Silicate	Nutrient flux ~ IP _{c,WM}
		Phosphate	Nutrient flux ~ AFDM + Manipulation + Sediment + AFDM:Sediment + Manipulation:Sediment

needs further confirmation, future models of nutrient fluxes across the sediment–water interface should in any case profit greatly from incorporating trait-based descriptions of macrofaunal irrigation behaviour.

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