RESEARCH ARTICLE

Seagrass is protected from ragworm pressure by a newly discovered grazer–ragworm interaction; implications for restoration

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Abstract

1. Coastal ecosystems are generally controlled by the combination of bottom-up (resource-driven) and top-down (consumer-driven) trophic, and non-trophic interactions. Anthropogenic disruption of these interactions, for example, through eutrophication or overfishing, leads to loss of the foundation species composing these ecosystems. Within degraded ecosystems, new interactions may become dominant, hampering restoration of the foundation species.

2. We demonstrate this concept in saltwater Lake Grevelingen, where seagrass restoration was seriously hampered by a newly discovered non-trophic interaction between the seagrass *Zostera marina* and the ragworm *Platynereis dumerilii*. *Platynereis* constructs dwelling tubes between seagrass leaves by glueing and entangling them, leading to loss of biomass and increased epiphyte cover. To test the roles of epiphyte grazing (top-down) and eutrophication (bottom-up) on this new-found interaction, we executed a field experiment introducing the snail *Littorina littorea* under natural nutrient concentrations and *Platynereis* densities and performed a full factorial mesocosm experiment applying *Littorina*, *Platynereis* and nutrient treatments.

3. Our field results show that survival of reintroduced *Zostera* in Lake Grevelingen is seriously hampered by *Platynereis*, which can be suppressed by grazer addition.

4. In our mesocosm experiment, we demonstrate that top-down control by *Littorina* protects seagrass through two pathways: (1) mitigating bottom-up regulated epiphyte growth by trophic top-down forcing and (2) hampering the non-trophic interaction between *Zostera* and *Platynereis* by grazing epiphytes and dwelling tubes.

5. *Synthesis and applications*. With coastal ecosystems globally under pressure, our study emphasises the importance of understanding ecosystem-specific trophic and non-trophic key interactions when considering restoration. We show how

negative interspecific interactions can become dominant in degraded systems with absent key facilitating interactions. Next, we show that these negative interactions (leaf glueing), inhibiting foundation species restoration, can be overruled by active inclusion of a key facilitating interactions (epiphyte grazing by mesograzers). Finally, we provide a three-step co-introduction approach for restoration management.

1 | INTRODUCTION

Coastal ecosystems (e.g. coral reefs, seagrass beds, mangrove forests, salt marshes, oyster reefs) are often formed by foundation species, supporting biodiversity, coastal protection, carbon sequestration, nutrient cycling and recreation (Angelini et al., 2016; Whitfield, 2017). They are, however, in rapid global decline, often associated with eutrophication, climate change, coastal development and overfishing (Waycott et al., 2009). These anthropogenic disturbances generally also affect ecosystem structure and interspecific interactions (Östman et al., 2016). More specifically, they can alter trophic interactions, bottom-up (resource-driven) and top-down (consumer-driven) and non-trophic interactions, which together regulate the stability of these ecosystems (Garbary et al., 2014; Moksnes et al., 2008; Östman et al., 2016; Valdemarsen et al., 2011; Whalen et al., 2013). Changes in key interactions can, in turn, cascade into further destabilisation of foundation species, ecosystem degradation and eventually the loss of ecosystem functioning.

Clear examples of these changing interactions, and their effects, can be found in many coastal ecosystems shaped by habitat-forming foundation species. In kelp forests, overexploitation of sea otters relieved sea urchins from predator pressure and resulted in the elimination of macroalgae (Estes et al., 1978). In salt marshes, overfishing of blue crabs released marsh periwinkles from predation, resulting in higher grazing pressure on marsh plants which led to barren mudflats (Silliman & Bertness, 2002). In seagrass beds, predation pressure by mesopredators on mesograzers can allow for algae blooms to occur which compete with seagrass for light and nutrients (Östman et al., 2016; Whalen et al., 2013). Positive non-trophic interactions, mainly established via the habitat-modification capabilities of the foundation species (Borst et al., 2018; van der Heide et al., 2011), are affected by anthropogenic factors as well. For example, the removal of oyster reefs can inhibit the long-distance facilitating effect on salt marshes, making them more prone to wave energy (Gribben et al., 2019; Meyer et al., 1997). In these destabilised systems, negative non-trophic interactions can become dominant as well; seed burial by lugworms *Arenicola marina* inhibits seagrass recruitment in recently degraded systems (Valdemarsen et al., 2011) and introduced invasive shore crabs *Carcinus maenas* clip seagrass shoots (Garbary et al., 2014). Although highly important, much about the interaction between changing trophic and non-trophic interactions

among coastal ecosystem-associated species and the effect on their foundation species remains unknown.

A recently discovered non-trophic interaction between eelgrass *Zostera marina* L. (hereinafter referred to as *Zostera*) and the ragworm *Platynereis dumerilii* (hereinafter *Platynereis*) showed that efforts to restore *Zostera* in Lake Grevelingen were severely inhibited by the 'glueing' behaviour of *Platynereis* (Cronau et al., 2022). *Platynereis* is globally distributed and often found in seagrass meadows (Daly, 1973; Gambi et al., 2000; Jacobs & Pierson, 1979; Riera et al., 2020). *Platynereis* is known to glue algal thalli together by the construction of dwelling tubes, used as a refuge against predators (Daly, 1973; Gambi et al., 2000). At our restoration site, we found that glueing of *Zostera* leaves significantly hampered planting unit survival and increased epiphyte growth (Cronau et al., 2022). The latter is likely explained by a behaviour called algae gardening, where *Platynereis* attaches epiphytes to its dwelling tube for later consumption and structural consolidation (Bedford & Moore, 1985; Gambi et al., 2000). It can be speculated that this interaction between *Zostera* and *Platynereis* has become more dominant because anthropogenic disturbances caused drastic shifts in species composition in Lake Grevelingen. That is, large predatory fish decreased while polychaeta and benthic fish species increased (Tangelder et al., 2019). Moreover, the gastropods *Hydrobia ulvae* and *Littorina littorea* (hereinafter *Littorina*), both important epiphyte grazers, have almost disappeared (Hoeksema, 2002). These shifts in species composition are similar to those found in other seagrass ecosystems (Moksnes et al., 2008; Riera et al., 2020). As interspecific interactions are increasingly being recognised as crucial for seagrass conservation and restoration (Gagnon et al., 2020; Sievers et al., 2022), the mechanisms responsible for the dominant negative interaction between *Platynereis* and *Zostera* found in Lake Grevelingen should be clarified. Moreover, recognising these mechanisms in an early stage could prove important for timely conservation management or increased restoration success.

To mechanistically understand how and why *Platynereis* was found to affect *Zostera* growth and how epiphyte grazing by *Littorina* affects this interaction under nutrient enriched and non-enriched conditions, we conducted a field experiment and a mesocosm laboratory experiment. We tested the following hypotheses: (1) non-trophic leaf-glueing by *Platynereis* negatively affects seagrass performance, (2) nutrient enrichment (bottom-up forcing) increases

epiphyte growth, and thereby increases the negative impact of *Platynereis* glueing on seagrass performance, (3) grazing by *Littorina* (top-down forcing) decreases epiphyte cover, and thereby counters the negative effect of leaf-glueing by *Platynereis* and nutrient enrichment. In the field experiment, we studied the effect of *Platynereis* on *Zostera* survival under naturally occurring *Platynereis* densities and tested the impact of addition of *Littorina* in a system all but devoid of gastropod grazers. In the laboratory experiment, we examined the interacting effects of *Platynereis*, *Littorina* and nutrient addition on plant performance, using a controlled, full factorial design.

2 | MATERIALS AND METHODS

2.1 | Study area and species

Our field experiment was conducted at Lake Grevelingen, the Netherlands (Figure 1a). Covering about 10,800 ha, the lake was formed from a former estuary in 1971 and consists of sand banks and deep channels. Nowadays, water-level amplitude is only about 5 cm and salinity varies between 27.7 and 31.6 psu throughout the lake due to the small opening in the Brouwers dike connecting the lake with the sea, as well as surface runoff from the surrounding land (van Donk et al., 2021). Historically, *Zostera* occurred in low abundance, but started dominating simultaneously with a drop in salinity shortly after the lake was dammed, extending to a maximum coverage of 4600 ha in 1978. *Zostera* disappeared again in the late 1990s, most likely caused by human driven salinity shifts forming a bottleneck for the present seagrass population that had adapted to a less saline environment (van Katwijk et al., 2023). Currently, no seagrasses have remained for natural recolonisation, and ephemeral macroalgae have taken over the role of dominant primary producers within the lake.

Whilst *Littorina* numbers have declined to values below 1 m^{-2} in Lake Grevelingen, *Platynereis* is one of the most numeric species with reported local average densities of 490 m^{-2} (Sistermans et al., 2006). These trends are found around multiple seagrass and algae systems globally (Hughes et al., 2004; Monroy-Velázquez et al., 2019; Riera et al., 2020). Natural densities of both species are highly variable and vary from 0 to up to 2000 m^{-2} for *Platynereis* (Table S3) and from 0 up to 200 m^{-2} for *Littorina* (Saier, 2000) in subtidal areas. Both *Littorina* and *Platynereis* are known to inhabit the littoral and subtidal coastal areas, relying on hard substrate, and are mainly found on depths ranging from 0 to 1 and 0 to 3 m deep, respectively, with *Platynereis* observed at depths up to 80 m deep (Gambi et al., 2000). Their geographic distribution is mainly focused around the Northern Atlantic Ocean, but *Platynereis* has been found to show an almost cosmopolitan distribution with occurrences on all continents except Antarctica (GBIF.org, accessed 2022). Reproduction of both species varies, due to their widespread distribution, but is known to occur between winter and spring in Europe (Barroso et al., 2007; Bedford & Moore, 1985).

2.2 | Field experiment

2.2.1 | Design

To test the effect of grazing on *Platynereis* leaf-glueing during *Zostera* restoration under natural circumstances, we conducted an enclosure experiment containing an epiphyte grazer addition, a control and a no-enclosure control treatment at two different sites within Lake Grevelingen, with a historic presence of *Zostera*; Veermansplaat (VP; 51°44′55.6578″N, 4°0′10.548″W) and Sirjansland (SJ; 51°41′19.2228″N, 4°1′6.2358″W) (Figure 1a). The two sites were selected at depths ranging from 90 to 110 cm, similar to the depth of highest historical *Zostera* coverage in Lake Grevelingen (Nienhuis et al., 1996). Both sites were relatively sheltered from the dominant southwest winds. Permission for conducting the fieldwork at these sites was provided by Rijkswaterstaat and Staatsbosbeheer, which are both managers of Lake Grevelingen. No ethical approval was required for conducting the experiments presented in this paper.

2.2.2 | Species collection and setup

Zostera ramets were harvested at Limfjord, Denmark (57°0′57.69736″N, 9°29′23.0172″E) at a depth of approximately 80 cm on 12 June 2019. Ramets were carefully collected and rinsed from sediment. The cleaned ramets were stored in crates covered with wet cloths to keep them moist during transport. After transport, the ramets were stored in aerated basins filled with artificial sea water. The next day, planting units were created by bundling three ramets using iron wire, attaching them to a 15-cm iron nail. All shoots were selected to have at least three living leaves and a rhizome containing intact roots. The experiment started on 14–15 June 2019, when 720 planting units (2160 shoots) were evenly distributed over 30 plots (15 plots per site) with 24 planting units (72 shoots) m^{-2}. Planting units were planted in a 5×5 pattern with the first planting slot replaced by a 1 m long rebar marker. Each plot was enclosed within a cage (1.13 m^2, 1 m high), constructed from a perforated (5 mm holes) aluminium sheet. The cages were pushed 10 cm into the sediment and anchored with three 1.5 m long rebars. Next, five plots per site were given a grazer treatment by adding 250 specimens of *Littorina* per plot (Figure 1b), based on the densities in the Limfjord seagrass meadow and known to significantly improve *Zostera* productivity (Jaschinski & Sommer, 2011).

2.2.3 | Monitoring

Plots were visited monthly by snorkelling for minimal disruption. *Littorina* were replenished when counts dropped below 100 per plot. *Littorina* density, planting units, planting units containing leaves glued by *Platynereis* (Figure 1c), total leaf count and glued leaf count were quantified.

FIGURE 1 (a) Study area and field sites; (b) cage enclosing *Littorina*; (c) planting unit with leaves glued together by *Platynereis* and extensive epiphyte growth (Cronau et al., 2022); (d) *Platynereis* treatment in the lab showing entangled old and young leaves covered with epiphytes; (e) *Littorina* treatment showing free spaced leaves and little epiphyte growth.
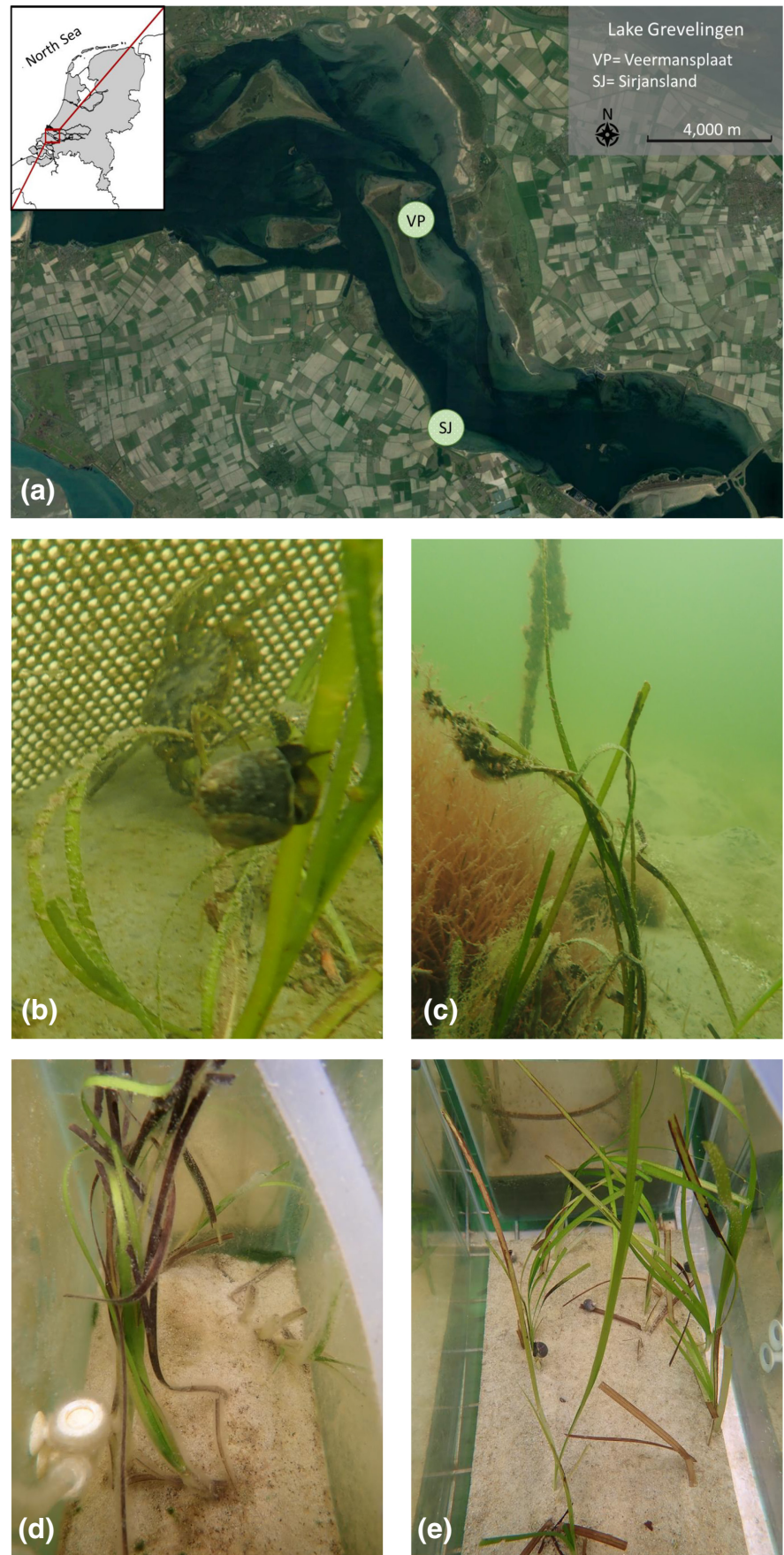
2.3 | Laboratory experiment

2.3.1 | Design

To mechanistically test how *Platynereis*, *Littorina*, eutrophication and their combinations affect *Zostera*, we conducted a full factorial experiment in which we manipulated *Platynereis* (P), nutrients (N) and *Littorina* (L). This resulted in eight treatments: control (C), P, N, L, PN, PL, NL and PNL within four aquaria ($35 \times 20 \times 50$ cm) replicates. *Platynereis* treatments received 18 *Platynereis* per aquarium (Figure 1d), resulting in a density of $257\,m^{-2}$, which is within ranges observed in Lake Grevelingen. Nutrient treatments received a concentration of $10\,\mu mol\,L^{-1}$ PO_4, $45\,\mu mol\,L^{-1}$ NH_4 and $15\,\mu mol\,L^{-1}$ NO_3 by adding NaH_2PO_4, NH_4CL and $NaNO_3$, respectively, based on the highest surface water nutrient levels observed during the field experiment as well as other available Lake Grevelingen data (Table S1; waterinfo.rws.nl). *Littorina* treatments received 20 *Littorina* per aquarium (Figure 1e), similar to the density of our field experiment.

2.3.2 | Species collection

Seagrass ramets were harvested and transported on 10 October 2019 using the same method and location as for the field experiment. Within the donor bed, *Littorina* were handpicked and transported in a closed container and aerated during transport. After transportation, *Zostera* and *Littorina* were placed in reservoirs with artificial seawater (Tropic Marin Inc.; 28 psu) and ramets were planted in natural sediment from Lake Grevelingen for acclimatisation (18°C; 14 h light, 10 h dark). Artificial light was provided at 160–205 $\mu mol\,m^{-2}\,s^{-1}$ (photosynthetic photon flux density; at mid-depths of aquaria) to reach light requirements for optimal *Zostera* growth (Olesen & Sand-Jensen, 1993).

Platynereis were collected at Lake Grevelingen on 23 October, by handpicking free-floating macroalgae, mainly *Sargassum muticum*. After transportation, they were carefully removed and placed in water reservoirs filled with artificial seawater at 12°C as well as shells and *Sargassum* serving as a natural substrate and food source.

2.3.3 | Experimental setup

Aquarium water consisted of 90% artificial seawater and 10% natural Lake Grevelingen water (28 psu) to introduce naturally occurring epiphytes. Salinity was maintained stable by adding demineralized water to counter evaporation. The nutrient treatment was applied continuously through a flowthrough system driven by Masterflex pumps which refreshed the water column weekly. Each aquarium was equipped with a CO_2-pump for pH control (7.5–7.9 pH) to balance CO_2/HCO_3^- in aquaria for similar potential photosynthetic capacity. Constant water circulation was guaranteed by a water pump circulating water that passed a UVC-lamp to prevent phytoplankton blooms (Figure S1).

The aquaria were placed in a randomised block design with a total of 4 blocks. *Zostera* ramets selected for the experiment consisted of a single apical shoot with a minimum of three leaves, including one young leaf (<10 cm) and a 4 cm rhizome. Wet weight per ramet was measured after which they were evenly distributed in groups of six ramets per aquarium and gently placed in a layer of 5 cm sieved sediment (1 mm mesh) from Lake Grevelingen. Subsequently, the sediment was capped with a 1-cm layer of silver sand to reduce nutrient leakage. Finally, *Littorina* and *Platynereis* were evenly distributed according to size, and the nutrient treatment was added to the water reservoirs.

2.3.4 | Monitoring and maintenance

Every ~10 days, we monitored the number of leaves, glued leaves, *Platynereis* bite marks, and percentage of epiphyte cover per ramet. Salinity and pH were checked daily and adjusted when necessary. To keep the grazing pressure stable, we replaced dead *Littorina* from a stock. On day 70, we terminated the experiment. *Zostera* roots and shoots were washed, and leaves were cleaned from epiphytes using a razor blade. Plants were dissected in below-ground and above-ground parts, and number of shoots per ramet and leaves per shoot were counted. Biomass was dried at 70°C for 48 h for dry weight measurement.

2.4 | Statistical analysis

For the field experiment, first, the cage effect on percentage glued leaves was analysed using a generalised linear mixed model (GLMM) with cage addition and time as explanatory variables and plot as a random effect to account for repeated observations over time. Second, *Littorina* treatment effect on the percentage of glued leaves was analysed likewise, with *Littorina* treatment replacing cage addition, omitting the non-cage treatment from the model. Third, *Littorina* effect on planting unit count during the last monitoring round was analysed using a generalised linear model (GLM) with *Littorina* treatment as an explanatory variable.

For the laboratory experiment, epiphyte cover and glueing percentage were averaged per aquarium and analysed using GLMMs. The interaction terms of treatments as well as time were included as explanatory variables, and the aquarium was incorporated as random effect to account for the repeated observations over time. The same model was run for *Platynereis* bites per aquarium. Only *Platynereis* treatments were included for the glueing and bites model. Responsive *Zostera* variables (i.e. shoots and leaves per ramet, and below-ground dry weight) were averaged per aquarium and analysed using LMs containing the interaction terms of the treatments as explanatory variables. Laboratory experiment analyses were

followed by a posteriori multiple-comparison test (Tukey HSD) with Benjamini–Hochberg corrections using the glht function within the MULTCOMP package (Hothorn et al., 2008).
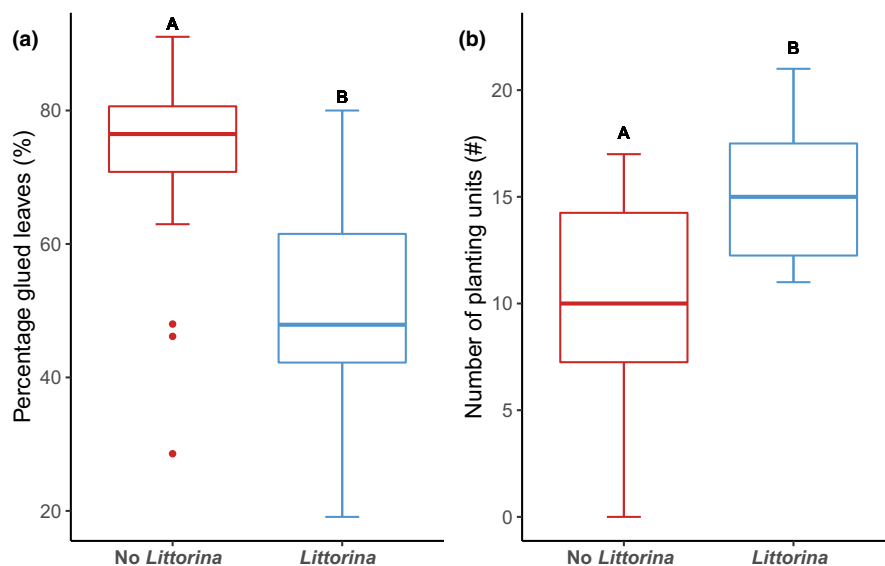
Distributions of GL(M)Ms were adapted according to their data family. Responsive variables were log +1 transformed and log (upper bound +1 − x) transformed in the case of an upper-bound left-skewed distribution, when necessary to meet the assumptions of the corresponding statistical test. Poisson models were checked for overdispersion. P-values were retrieved with the ANOVA and Anova command (CAR package; Fox & Weisberg, 2018) for L(M)M and GL(M)M, respectively, using Type III analysis for models containing interaction terms. All tests were considered significant at an alpha level of $p \leq 0.05$. Means in text and figures are followed by the standard error (SE). Statistical analyses were conducted in R v4.2.0 (R Core Team, 2021).

3 | RESULTS

3.1 | Field experiment

Each plot contained *Zostera* plants with leaves glued by epiphyte-covered *Platynereis* tubes. No significant effect of cage addition was found. However, number of glued leaves showed a significant interaction with time, with the addition of cages resulting in slightly more glued leaves during the first moment but slightly less during the second ($F_{(1, 35)} = 5.45$; $p = 0.025$). When considering cage-containing plots, the percentage of glued leaves was high and similar between sites, with a mean ($\pm$ SE) of $61.14 \pm 4.28\%$ ($n = 19$), and $61.04 \pm 4.28\%$ ($n = 20$) for SJ and VP, respectively, and constant over time. However, during this period the percentage of glued leaves was strongly reduced in the *Littorina* treatment ($F_{(1, 22.8)} = 15.43$, $p = 0.007$; Figure 2a) by $21.3 \pm 6.6\%$. At the end of the experiment, the *Littorina* treatment demonstrated a 58.3% higher plant survival ($Chi = 9.91$, $p = 0.002$) compared to controls (Figure 2b). Additionally, the density of planting units had decreased to 10.2 ± 1.5 m^{-2} in control plots compared with 15.2 ± 1.1 m^{-2} in *Littorina* plots.

3.2 | Lab experiment

3.2.1 | Epiphyte cover

Epiphyte cover on *Zostera* leaves increased over time ($F_{(6, 144)} = 67.41$; $p < 0.001$) in all treatments from virtually clean to $27.00 \pm 1.57\%$ (range: 0%–90%) at the end of the experiment (Figure 3a; Table S2). Nutrient treatment increased epiphyte cover ($F_{(1, 24)} = 10.51$, $p = 0.003$), while *Littorina* treatment reduced this ($F_{(1, 24)} = 167.97$, $p < 0.001$) and was able to fully halt the increase in epiphyte cover until the end of the experiment. Both the nutrient and *Littorina* treatment showed an interaction with time ($F_{(6, 144)} = 3.20$, $p = 0.006$; $F_{(6, 144)} = 8.77$, $p < 0.001$). Nutrients especially increased epiphyte cover in the first weeks after which it plateaued, while *Littorina* suppressed epiphyte growth early in the experiment with only a slight increase after a few weeks.

3.2.2 | *Platynereis* effects

All *Platynereis* treatments showed immediate glueing of leaves. After 6 days, the treatments started to diverge ($F_{(1, 12.82)} = 18.75$, $p < 0.001$; Figure 3b; Table S2). Most importantly, the *Littorina* treatment reduced leaf-gluing ($F_{(1, 12.82)} = 47.21$, $p < 0.001$). This mitigating effect was even stronger after nutrient addition, resulting in a *Littorina*–nutrient interaction ($F_{(1, 12.82)} = 4.91$, $p = 0.045$).

During the experiment, *Platynereis* took bites of *Zostera* leaves, which was only noticed in *Platynereis* treatments at $t = 27$ days (Figure S2). The nutrient treatment reduced the number of bites ($Chi = 4.12$, $p < 0.043$), while the *Littorina* and nutrient treatment interacted ($Chi = 5.25$, $p < 0.022$), with *Littorina* cancelling out the nutrient effect.

3.2.3 | Plant response

At the end of the experiment, shoot counts per ramet differed between treatments (Figure 4a), with a significant effect of *Littorina*

FIGURE 2 Boxplots of field experiment showing (a) percentage of glued Zostera leaves per plot during August and September ($n = 39$) and (b) number of survived planting units per plot during September ($n = 19$). Medians with quartile ranges. Significant differences indicated by different letters.
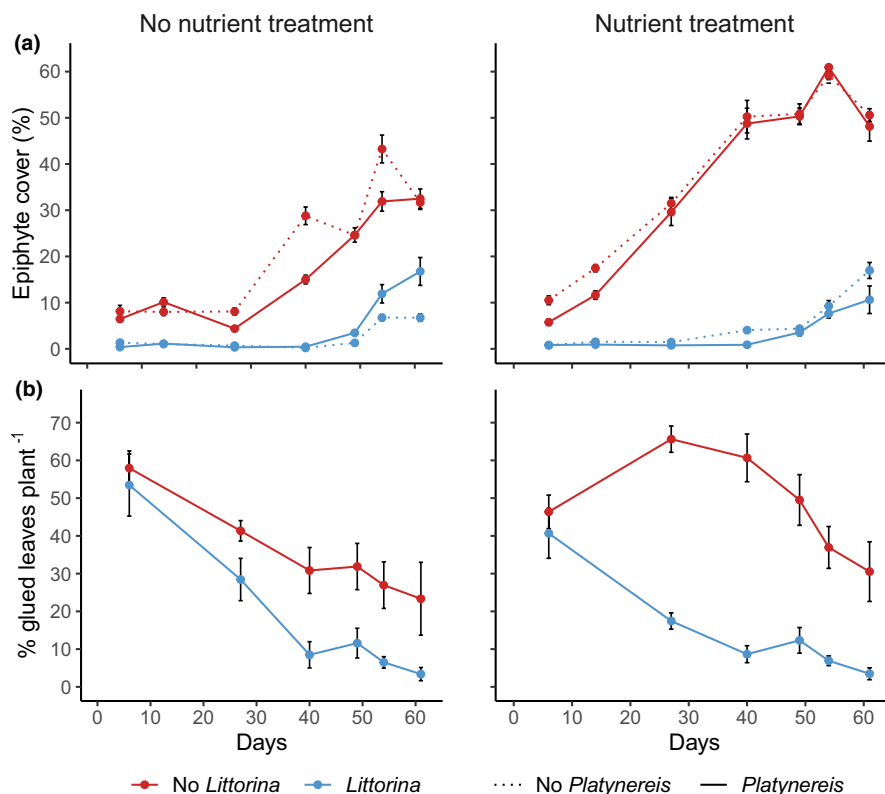
FIGURE 3 Line graphs of lab experiment showing the Mean (± SEM) percentage of (a) *Zostera* surface covered by epiphytes over time; (b) percentage of glued leaves over time for the different *Platynereis* treatments.

treatment ($F_{(1, 24)}$ = 5.662, p = 0.026). We also found an interaction between the *Littorina* and *Platynereis* treatment ($F_{(1, 24)}$ = 9.183, p = 0.006), where *Littorina* countered the negative effect of *Platynereis* on the number of shoots per ramet. For leaves per ramet, significant effects of *Littorina* ($F_{(1, 24)}$ = 20.08, $p < 0.001$) and *Platynereis* ($F_{(1, 24)}$ = 4.31, p = 0.049) were found as well as an interaction between both treatments ($F_{(1, 24)}$ = 16.36, $p < 0.001$) with *Littorina* fully countering the negative effect of *Platynereis* on the leaf count per ramet (Figure 4b). For both parameters, no effect or interaction with the nutrient treatment was found.

Similarly to previous variables, the *Littorina* treatment increased below-ground dry weight ($F_{(1, 24)}$ = 23.87, $p < 0.001$) and interacted with the *Platynereis* treatment ($F_{(1, 24)}$ = 19.71, $p < 0.001$) fully countering its adverse effects (Figure 4c). Contrasting with other response variables; however, the nutrient and *Littorina* treatment interacted ($F_{(1, 24)}$ = 9.82, p = 0.005) with a stronger *Littorina* effect under enriched conditions.

4 | DISCUSSION

Our results show that *Zostera* survival is strongly controlled by the newly discovered interaction between *Littorina* and *Platynereis*. Our field experiment showed top-down control by *Littorina* to mitigate the negative non-trophic interaction of *Platynereis* on *Zostera* within Lake Grevelingen, a system that is presently largely devoid of epiphyte grazers. This interaction was in line with our hypothesis and was confirmed by our lab experiment. Here, we found that *Littorina* protects seagrass through two distinct pathways: (1) mitigating

bottom-up regulated epiphyte growth by trophic top-down forcing and (2) hampering the negative non-trophic *Platynereis–Zostera* interaction. We suggest that the interaction between *Littorina* and *Platynereis* potentially plays an important role in many North Atlantic seagrass systems given their wide distribution, especially with coastal ecosystems changing due to anthropogenic disturbances. Moreover, our findings emphasise the importance of a healthy mesograzer population and the potential of co-introduction as a method to increase restoration success.

4.1 | Top-down control of nutrient enrichment by *Littorina*

In our lab experiment, we observed an increase in fast-growing epiphyte cover which was positively affected by bottom-up forcing through nutrient enrichment. Extensive epiphyte growth in systems released of top-down control is well reported (Littler et al., 2006; Whalen et al., 2013), and top-down control by *Littorina* grazing in our mesocosms reduced epiphyte cover within non-enriched and enriched treatments alike (Figure 5). Top-down control by grazers is known to relieve coastal ecosystems from bottom-up forcing (Östman et al., 2016; Whalen et al., 2013) and in many healthy coastal ecosystems, they regulate communities, maintaining ecosystem structure and stability (Estes et al., 2004; Littler et al., 2006). In seagrass meadows, epiphyte grazing favours seagrass by the release of competition for nutrients and light (Hughes et al., 2004). However, both anthropogenic increased bottom-up forcing (nutrient enrichment) and decreased top-down forcing (grazer absence) destabilise

FIGURE 4 Boxplots of lab experiment showing (a) number of shoots ramet^{-1}, (b) number of leaves ramet^{-1} and (c) below-ground dry weight ramet^{-1} after 70 days (all including dead ramets with 0 shoots). Means per aquaria represented in quartile ranges ($n = 4$). The non-nutrient treatments: (C) Control, (L) *Littorina*, (P) *Platynereis*, (PL) *Platynereis*:*Littorina* are represented on the left panel and nutrient treatments (N) Nutrient, (NL) Nutrient:*Littorina*, (PN) *Platynereis*:Nutrient and (PNL) *Platynereis*:Nutrient:*Littorina* on the right panel. Significant differences are indicated by different letters.
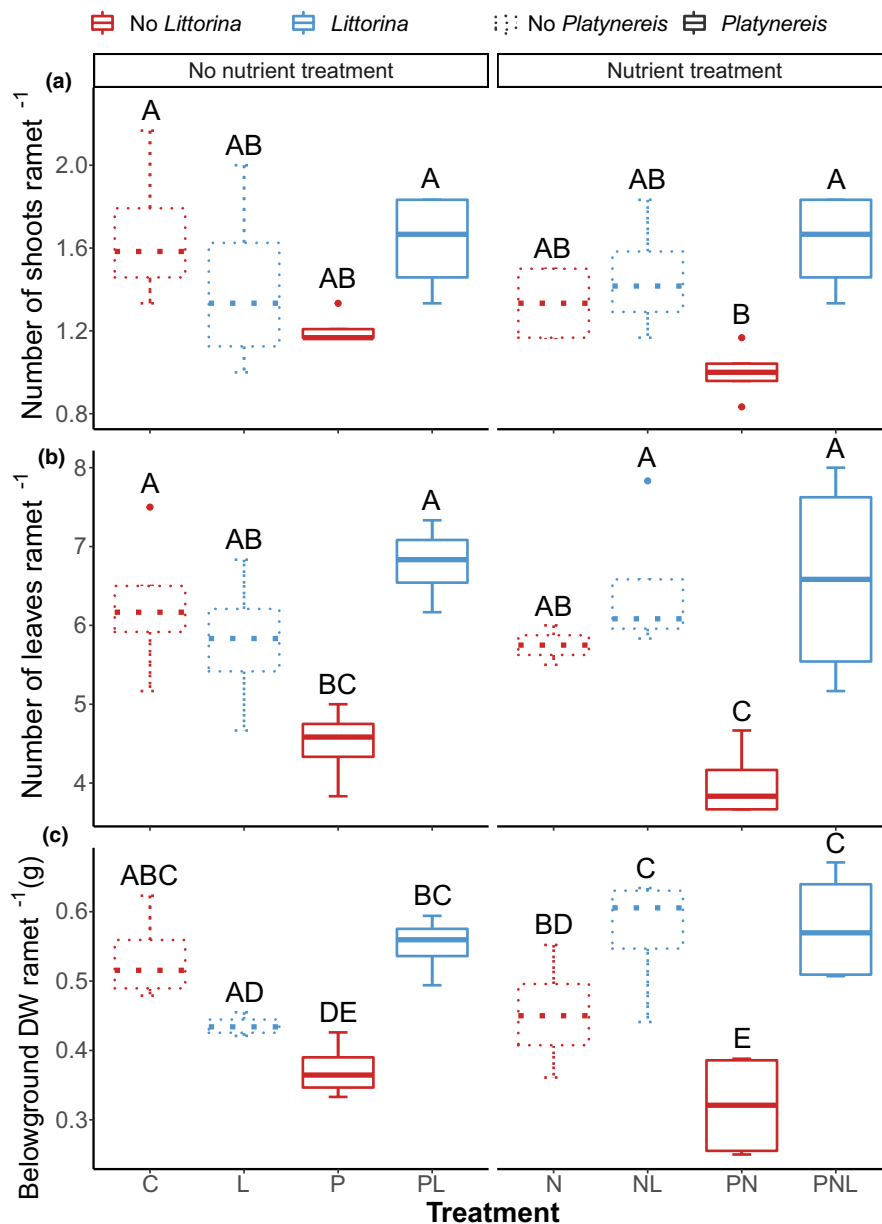
this balance in favour of algae at the expense of the foundation species, as simulated by our lab experiment.

4.2 | Effects of *Platynereis dumerilii* on seagrass

Platynereis glued seagrass leaves together in the field and lab study, resulting in entangled plants with dead leaves still attached (Figure 1c,d). This non-trophic behaviour was previously observed only in macroalgae (Bedford & Moore, 1985) and was only recently discovered in seagrasses during a restoration study in Lake Grevelingen (Cronau et al., 2022). In accordance with Daly (1973), *Platynereis* began tube construction within a matter of minutes in the lab. After 6 days, seagrass leaves had been glued together in all *Platynereis* treatments. Epiphyte cover, however, was not higher in *Platynereis* treatments, contrasting with field observations by Cronau

et al. (2022). This could be explained by a lack of algae gardening in the lab with a less diverse epiphyte community compared with the field (Figure 1c,d). *Platynereis*, however, did consume epiphytes present in our lab experiment and the number of observed half-moon-shaped leaf bites, typical for *Platynereis* (Gambi et al., 2000), was increased by the *Littorina* treatment, where epiphyte cover was lowest, suggesting a partial diet shift from epiphytes to seagrass with epiphytes becoming limiting.

Although glueing by *Platynereis* did not increase epiphyte cover in the lab, it decreased the number of shoots and leaves per ramet, as well as below-ground dry weight. Glueing directly decreased effective leaf surface, mobility, and spacing of the leaves (Figure 1c,e). We argue that this, similar to epiphyte cover, has negative consequences for acquisition of both nutrients and light (Sand-Jensen, 1977). Limited nutrition and light are known to reduce above- and below-ground growth (Carroll et al., 2008) and the shedding of leaves
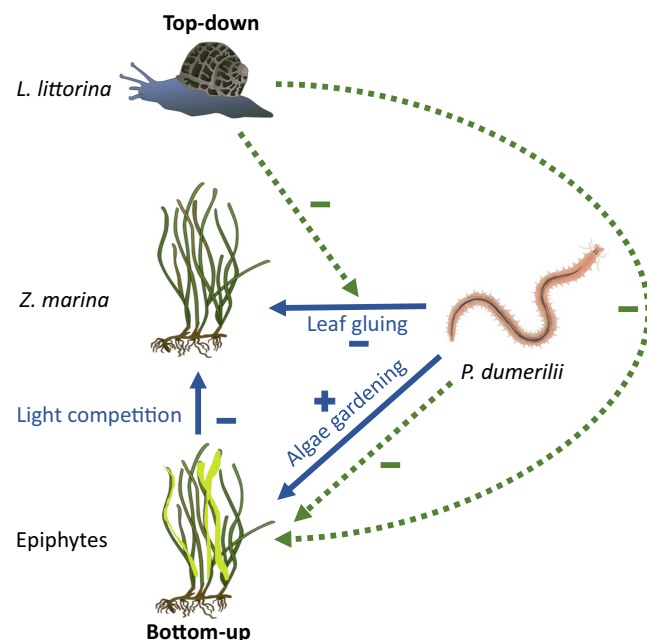
FIGURE 5 Interaction web of the top-down and bottom-up effects in our studied *Platynereis* and *Zostera* interaction. The top-down grazer is the snail *Littorina*; bottom-up forcing by nutrient enrichment increases algal epiphyte growth. Green dashed lines represent trophic interactions, whereas blue solid lines represent non-trophic interactions. While trophic interactions are consumer-resource-based, non-trophic interactions are named; see main text for further description. Symbols: ian.umces.edu.

(McMahon et al., 2013). In the field, glueing by natural densities of *Platynereis* led to a decrease of surviving planting units, showing that entanglement can even be harsher under natural conditions. Species of *Carcinus* and *Arenicola* also harm their associated foundation species through non-trophic interactions (Garbary et al., 2014; Valdemarsen et al., 2011). These are known to become problematic under already disrupted environmental conditions where the community composition shifts in favour of the disruptors (Eriander et al., 2016; Valdemarsen et al., 2011). In our study, this effect is visible with the absence of epiphyte grazers, allowing for the damaging effects of *Platynereis* activity.

4.3 | Dual protection of seagrass by *Littorina*

Our results show that the inclusion of an epiphyte grazer mitigates the negative effects of *Platynereis* on seagrass. In both the field and lab experiments, *Littorina* increased plant survival by reducing leaf glueing. This positive effect was amplified under nutrient-enriched conditions. *Littorina* also offset the negative effect of increased epiphyte growth on below-ground biomass under nutrient enrichment, and allowed for the increased nutrient availability to positively affect below-ground biomass (Figure 4c). It is already known that *Littorina* releases seagrasses from competitive pressure by epiphytes (Hughes et al., 2004), which is amplified under increased nutrient loading (Östman et al., 2016). However, our study reveals another, previously

unknown, protective pathway of *Littorina* through mitigation of the negative effects of *Platynereis* on *Zostera* (Figure 5). We observed both signs of exploitative competition for epiphytes between *Littorina* and *Platynereis* and interference competition with *Littorina* consuming the constructed tube of *Platynereis*. Both *Platynereis* and *Littorina* are known to consume algae (Gambi et al., 2000; Hughes et al., 2004) and, thus, naturally compete. *Littorina* consumes epiphyte assemblages on *Zostera* leaves unselectively by scraping the *Zostera* surface (Jaschinski & Sommer, 2008). Consequently, *Littorina* also consumes *Platynereis* tubes, which could prove paramount for the mitigation of the negative effects of *Platynereis* on seagrass. *Platynereis* abandons its dwelling every 2–3 days (Bedford & Moore, 1985) to relocate (Daly, 1973), increasing the potential negative effects of a single worm. However, through their continuous grazing, *Littorina* negates these effects by releasing glued leaves from old tubes. It remains to be investigated whether *Littorina* also grazes new tubes or whether *Platynereis* effectively defends occupied tubes.

Despite protecting *Zostera* plants, *Littorina* did not improve any of the plant parameters on its own in the lab. Instead, plant parameters appeared to be slightly adversely affected by the grazer treatment when applied in isolation, although not significant. An adverse effect of *Littorina* grazing on seagrass has previously been suggested through unselective scraping, incidentally destroying outer layers of *Zostera* leaves (Jaschinski & Sommer, 2008). Marsh periwinkles are also known to scar cordgrass leaves while grazing, resulting in high reductions in above-ground productivity (Silliman & Zieman, 2001). Based on the recorded grazing behaviour, similar negative effects from scraping could easily have taken place in our experiment.

4.4 | Implications for coastal ecosystem conservation and restoration

In this study, we show that seagrass-associated mesograzers are not only important for seagrass via trophic epiphyte control as previously documented, but that their role can be amplified through the control of *Platynereis*. In Lake Grevelingen, seagrass meadows declined along with key top predators such as cod *Gadus morhua* and grazers such as *Littorina* (Tangelder et al., 2019). This has also been documented in other coastal systems where the loss of top predators often resulted in a release of mesopredators, which in turn suppressed grazer populations, increasing competition between algae and seagrass (Baden et al., 2012; Hughes et al., 2013). In such systems, the (co-) introduction of mesograzers would improve seagrass survival and abundance, although the cause of mesograzer decline should also be alleviated. The latter could be achieved by reducing the density of mesopredators by targeted action such as mremoval or by restoration of the top predator population, which was shown to be effective in the facilitation of grazer populations (Hughes et al., 2013).

Another development in recent decades in Lake Grevelingen is the introduction and increase in blooms of the invasive exotic alga *S. muticum* (Tangelder et al., 2019). This may likely have enhanced the population density of *Platynereis*, as *Sargassum* is known to modify

epifaunal seagrass communities and is worldwide associated with *Platynereis* (Belattmania et al., 2018; Hunn et al., 2022; Monroy-Velázquez et al., 2019). Therefore, options to remove *Sargassum*, which is often exotic and invasive in the Atlantic Ocean, from these systems should be investigated.

The changes in trophic and non-trophic interactions as described above have already been detected in several systems in the Baltic Sea and Pacific Ocean (Baden et al., 2012; Hughes et al., 2013). We expect that this could potentially be happening in many more systems, as both *Littorina* and *Platynereis* are found in the entire North Atlantic, with *Platynereis* extending almost globally (GBIF.org, accessed 2022). Interestingly, grazer populations are often found to decrease, whereas *Platynereis* densities increase (Hughes et al., 2004; Hunn et al., 2022; Monroy-Velázquez et al., 2019; Riera et al., 2020; Tangelder et al., 2019). Therefore, we argue that pressure from high *Platynereis* densities on seagrass meadows may be on the rise and that this should be monitored more closely for timely intervention and, concurrently, that effective measures should be investigated for conservation and restoration purposes.

Recent studies increasingly emphasise the importance of facilitative interactions for coastal restoration success (Chin et al., 2021; Temmink et al., 2020; Valdez et al., 2020), and suggest active inclusion of key interspecific interactions during restoration for higher success rates (Derksen-Hooijberg et al., 2018; Gagnon et al., 2020; Sievers et al., 2022). Examples of direct positive interactions include the detoxification of sediment by Lucinidae in seagrass meadows or alleviation of drought stress for salt marsh plants by ribbed mussels (Angelini et al., 2016; van der Heide et al., 2012). Based on our findings and those of previous studies, we argue that, rather than trying to restore foundation species in isolation, co-introduction for the inclusion of key facilitative interactions should be considered when these are absent in the restoration area.

To improve seagrass restoration success in environments with degraded community structures, we propose a three-step strategy, followed by monitoring and evaluation, based on a restoration decision model suggested by Sievers et al. (2022): (1) Transplant seagrasses, preferably from a donor population with an intact food web, (2) co-introduce a (historically) native facilitating species to the system, preferably a dominant species from the same donor location (*Littorina* in our case) and (3) exclude inhibiting organisms directly (e.g. through manual removal; removal of *Sargassum* in our case) or indirectly (e.g. in our case, through facilitating trophic cascades; facilitating top predators).

Subsequently, regular monitoring of seagrasses, the co-introduced and excluded animals as well as used exclusion methods should be implemented to decide on potential repetition of the treatments.

AUTHOR CONTRIBUTIONS

Rens J. T. Cronau, Tjeerd J. Bouma, Jannes H. T. Heusinkveld, Dieuwke Hoeijmakers, Tjisse van der Heide conceived and designed the field experiment; Rens J. T. Cronau, Yvet Telgenkamp, Marieke M. van Katwijk, Tjisse van der Heide, Leon P. M. Lamers conceived and designed the lab experiment; Rens J. T. Cronau, Yvet Telgenkamp, Jannes H. T. Heusinkveld, Dieuwke Hoeijmakers performed the experiments; Rens J. T. Cronau, Jimmy de Fouw, Tjisse van der Heide analysed the data; Rens J. T. Cronau, Yvet Telgenkamp, Jimmy de Fouw, Marieke M. van Katwijk, Tjeerd J. Bouma, Tjisse van der Heide, Leon P. M. Lamers wrote and/or edited the manuscript.

CONFLICT OF INTEREST STATEMENT
The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT
Data are available from the DANS EASY Repository https://doi.org/10.17026/dans-x38-abzq (Cronau et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.