Basic and Applied Ecology 91 (2026) 17–25

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

Research Article

Recoupling terrestrial, benthic and pelagic habitats by constructing littoral zones diversifies carbon flows to aquatic macroinvertebrates

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ARTICLE INFO

Keywords:
Benthic food chain
Land-water transition zones
Habitat coupling
Habitat restoration
Light attenuation
Macroinvertebrate community
Organic matter fluxes
Stable isotope analyses
Shallow turbid lake
Wind-induced resuspension

ABSTRACT

Shoreline restoration measures are increasingly implemented to stimulate biodiversity recovery in degraded lake ecosystems. However, the underlying mechanisms of observed recovery processes often remain disclosed. Here, we mechanistically studied how the creation of littoral shorelines in a degraded pelagic-driven lake affected fluxes of organic material across shoreline gradients, which are known to be essential for the functioning of aquatic food webs. We assessed how new connections among habitat types (dry shorelines, littoral zones and the limnetic water column) affected carbon fluxes in the food web of the 70.000 ha large shallow turbid lake Markermeer (the Netherlands), to which 16% of soft sediment littoral shoreline was added by constructing 1300 ha of wetland islands in 2016. Development of islands and littoral habitats with water less than 1.5 m deep improved underwater light conditions compared to the surrounding turbid limnetic habitats of ~4 m deep, and therefore stimulated benthic primary producers. Field monitoring and stable isotope analyses revealed increases of benthic primary production and of organic material fluxes from the shoreline into the pelagic zone, which both stimulated the macroinvertebrate diversity. During the early phase of the restoration project (<8 years) benthic primary production transferred best to higher trophic levels compared to carbon-rich terrestrial material, likely due to the relatively higher quality of benthic food for macroinvertebrates. We conclude that the creation of sheltered shallow habitats in limnetic-dominated lakes can diversify carbon fluxes among habitats which stimulates the base of the aquatic food web. This makes lake restoration via re-coupling of terrestrial, pelagic and benthic habitats an effective forward-looking restoration measure for degraded monotonous lake ecosystems.

Introduction

Heterogeneity of habitat types at the landscape scale facilitates processes that overarch the boundaries of terrestrial, aquatic and marine ecosystems via habitat coupling (Schindler & Scheuerell 2002). Habitat coupling leads to exchange of energy, organic carbon, nutrients and organisms among habitats, and is essential for many species to thrive seasonally or complete sequential life stages (Stiling et al. 2023). Freshwater ecosystems rely on the mechanism of habitat coupling, as they exchange energy with their terrestrial surroundings as well as between benthic and pelagic habitats (Leal et al. 2023). Allochthonous processes in the littoral zones generate fluxes of terrestrial organic carbon from decaying plants into limnetic habitats, subsidizing benthic and pelagic organisms (Vannote et al. 1980; Cole et al. 2006). Simultaneously, autochthonous processes couple pelagic and benthic habitats by exchanging organic matter within lakes (autotrophic structure, Althouse et al. 2014, Vander Zanden & Vadeboncoeur 2020). Species in aquatic food webs therefore depend strongly on habitat coupling and are typically fuelled by combinations of organic matter from phytoplankton (pelagic), from periphyton and submerged macrophytes (benthic), or from the surrounding terrestrial landscape (Wetzel 1992, 2001).

The mechanism of habitat coupling is strongly impacted by anthropogenic activities involving large-scale morphological engineering of shorelines of rivers, lakes and seas (Brauns et al. 2007). Shoreline

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https://doi.org/10.1016/j.baae.2026.01.003
Received 12 September 2025; Accepted 14 January 2026

fortifications for water safety purposes, channelled water flows into lakes, or sand excavations uncouple energy flows typical for sheltered shallow littoral zones (Vadeboncoeur et al. 2002; Vander Zanden & Vadeboncoeur 2020; Tack et al. 2024). This decoupling can induce state shifts in lakes, from relying on diverse organic carbon sources towards relying primarily on pelagic primary production (Vadeboncoeur et al. 2008; Tack et al. 2024). The resulting shifts can have detrimental consequences for productivity at the base of the food web (Brothers et al. 2013), with cascading effects into higher trophic levels such as birds and fish relying on productive food webs and well-functioning littoral shore zones (Dolson et al. 2009; Pätzig et al. 2018; de Leeuw et al. 2024). So-called 'recoupling' of habitats in impacted freshwater ecosystems may therefore be highly beneficial to the base of aquatic food webs, but the effectiveness and mechanisms of this approach are less clear.

Habitat recoupling among terrestrial, pelagic and benthic habitats in littoral zones can likely be achieved by restoring the abiotic heterogeneity of the landscape. In 2016, a large-scale habitat restoration project called Marker Wadden was initiated with these aims in the degraded constructed lake Markermeer, located in a former coastal bay area in The Netherlands (van Leeuwen et al. 2021). Historic land reclamations, closure of the open connection to the North Sea (Afsluitdijk; 1930) and the construction of rip-rap dikes strongly lowered habitat heterogeneity and the coupling of processes on land and in the water (van Riel et al. 2019; van Leeuwen et al. 2021). This led to a lake ecosystem primarily driven by pelagic primary producers (Tack et al. 2024) and declines in bird and fish populations that are protected under Natura 2000 legislation. Since restoring the original estuarine conditions is not feasible due to newly acquired ecosystem services provided by the lake, the Marker Wadden is a forward-looking restoration project focussed on increasing the ecological integrity of the lake and its food web, without returning to former conditions (van Leeuwen et al. 2021, 2023, de Leeuw et al. 2024). For this project to successfully stimulate communities of higher trophic levels (i.e. fish and birds, Fig. 1), new missing sheltered littoral zones with gradual land-water transitions were created by constructing a 1300 ha archipelago in the open water of the 70.000 ha lake. This created a large area of littoral zones, that contrast strongly to the rest of the large lake consisting only of monotonic limnetic zones (4-meter-deep open water). Restoration measures were taken to (1) increase the productivity of the food web at lower trophic levels, including primary producers, zooplankton and macroinvertebrates, and (2) increase energy fluxes among pelagic, benthic and terrestrial habitats.

In order to trace these possible changes in trophic relations and energy fluxes in the food web, analyses of stable isotopes and elemental ratios can be used (Post 2002; Middelburg 2014). Because nitrogen isotope signals are transferred up to the consumers in the food web and carbon isotopes fractionate differentially between the littoral and pelagic habitats of lakes (Vander Zanden and Rasmussen 1999), primary producers can be linked to primary consumers. Due to the relatively higher investment in carbon-rich structural material of terrestrial plants compared to aquatic plants and the relatively low carbon availability in the water column, molar C:N ratios can furthermore be used to differentiate among terrestrial and aquatic primary producers (Leng and Lewis 2017). By combining analyses of δ^{13}C, δ^{15}N and C:N ratios, the coupling of terrestrial, pelagic and benthic food webs can be derived if carefully interpreted (Cloern et al. 2002; Middelburg 2014; Leal et al. 2023). Furthermore, isotopes can be used to assess the trophic niche breadth of organisms (Carscadden et al. 2020).

Here, our main aim is to assess how reconstructing sheltered littoral zones in the open water of a shallow lake ecosystem influences flows of energy and nutrients between habitats during the early years of new habitat creation. Therefore, we determined local impacts of restored land-water transitions and benthic-pelagic coupling on the flows of organic matter (containing both nutrients and energy) to the consumer community on restored littoral zones. Specifically, we compared the current situation in the open water of the large lake (further referred to as the limnetic zone) to the since 2016 restored situation with littoral habitat (further referred to as the littoral zone). We expected that the construction of sheltered littoral zones would decrease light attenuation by reducing wind-induced resuspension (Martinsen et al. 2022) and that a shallower water column would facilitate light availability on the sediment surface, which should together stimulate productivity by benthic primary producers (Brothers et al. 2013; Jin et al. 2022).

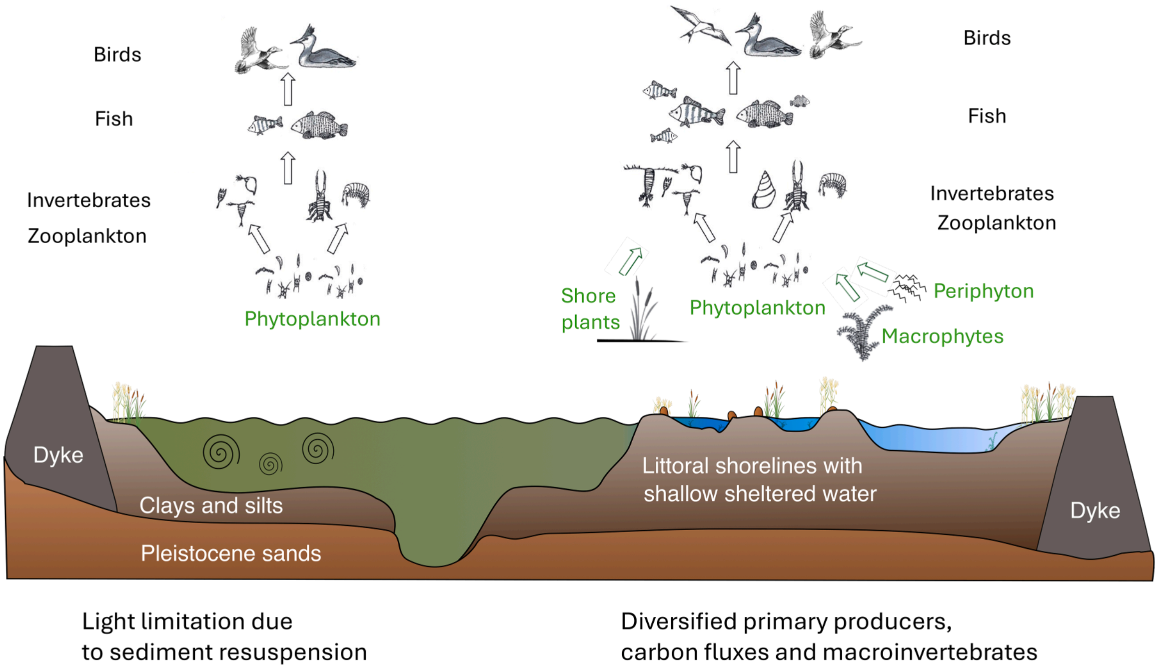

Fig. 1. Conceptual view of the expected influence of the new littoral zones with recoupled habitats on primary producers, macroinvertebrate primary consumers and higher trophic levels in Lake Markermeer, The Netherlands. Primary production in the original lake in the pelagic zone (left food web) is mainly driven by pelagic phytoplankton. In the new littoral zones (right food web), additional contributions of benthic (macrophytes and periphyton) and terrestrial (shore plants) primary producers are expected, forming a broader base of consumers and higher trophic levels in a more complex food web. Food web based on Jin (2021).

Simultaneously, we expected that productive terrestrial sites – newly connected to the limnetic system via gradual littoral shorelines – would enhance the influx of terrestrial organic carbon from decaying plants into the surrounding littoral habitats (Vander Zanden and Vadeboncoeur 2020). Last, we expected the new benthic and new terrestrial organic matter (OM) sources to both contribute to secondary production of aquatic macroinvertebrates and thus lead to an increase in potential food resources that would increase their trophic niche breadth. We studied their relative effects on the consumer community during the early phases of shoreline restoration.

Materials and methods

Lake Markermeer

Lake Markermeer is a constructed freshwater lake in the Netherlands, situated in the northern branches of the Rhine delta to the Wadden Sea (Fig. 2a). The lake was formed in a former marine estuary (called “Zuiderzee”)by a series of engineering activities, including (1) the construction of two >25 km long dikes that disconnected the Zuiderzee from the Wadden Sea and created one large freshwater lake; (2) a series of land reclamations that reduced the surface area and separated the water from land by rip-rap dikes; and (3) the separation of the large lake into two smaller lakes, called lake IJsselmeer (110.000 ha, still connected to the River IJssel) and our study lake Markermeer (70.000 ha, largely without riverine influence).

Lake Markermeer obtained the Natura 2000 status in 2009 due to its international importance for breeding and migrating bird populations (Rijkswaterstaat 2017). However, the lake is very homogeneous in abiotic conditions: it has a mean depth of ~4 m, the shorelines are dominated by rip-rap to reduce the impact of strong wind-induced wave action (van Riel et al. 2019; de Leeuw et al. 2024), and the lake’s soft sediment consisting of clays and silts create turbid conditions if winds induce resuspension (van Kessel et al. 2008; Vijverberg et al. 2011). This high turbidity creates a high light attenuation (K_d) and limits macrophyte establishment (Jin et al. 2022). Therefore, the lake’s productivity is largely dependent on primary production by phytoplankton in the pelagic zone (Tack et al. 2024), consisting partly of microalgae that grow on resuspended aggregates in the illuminated part of the water column (Brinkmann et al. 2019).

Restoration project Marker Wadden

The classical restoration option to increase the lost productivity of the constructed lake Markermeer would be to return to the conditions of the former Zuiderzee estuary, in which a heterogeneous mosaic of habitats formed a productive shallow coastal bay area with sufficient nutrient levels and connect aquatic and terrestrial ecosystems. However, since its formation, lake Markermeer has started to provide essential ecosystem services. These ecosystem services provided by the lake, including drinking water provisioning, water storage for irrigation, and flood safety (Gulati and van Donk 2002), would be compromised by classic restoration (van Leeuwen et al. 2021). Therefore, the addition of sheltered shallow littoral zones to the lake was proposed as a potential solution to boost its heterogeneity and with that broaden the lake’s productivity. Between 2016 and 2021, seven marshland islands were constructed in lake Markermeer with the aim to add a mosaic of shallow littoral zones, in which benthic and terrestrial producers would be stimulated to provide food for higher trophic levels including fish and birds. The islands were built by creating sheltered basins surrounded by ring dikes from locally deep extracted nutrient-poor Pleistocene sands, which were filled with locally extracted nutrient-rich soft clays and silts extracted from upper Holocene layers (van Leeuwen et al. 2021). The soft sediments were left to subside and consolidate for two to three years, after which the marshlands with shallow water inside the basins were connected to the open water of the lake. This way, the Marker Wadden project added 1300 ha of littoral habitat to the homogeneous limnetic lake, including 81 km of gradual shorelines connecting land and

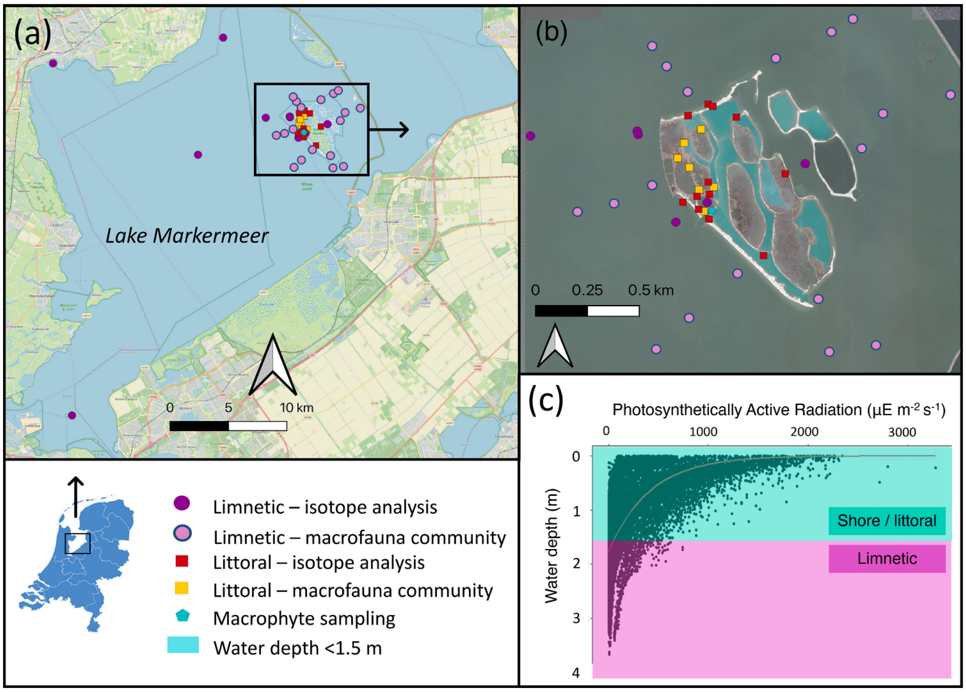

Fig. 2. (a) Lake Markermeer in the Netherlands with the sampling locations of isotope and community data indicated. The rectangle shows the location of the Marker Wadden in Lake Markermeer further detailed in panel b. (**b**) The Marker Wadden archipelago with the isotope and community data sampling locations. Turquoise shading indicates water depths shallower than 1.5 m. (**c**) Light availability in the form of Photosynthetically Active Radiation (PAR) at different water depths in lake Markermeer. The approximate shore / littoral and sheltered limnetic areas are indicated with turquoise and pink shading, respectively, which illustrates that PAR at the sediment surface in the 4 m deep open water is very low.

water (de Leeuw et al. 2024), and hundreds of hectares of sheltered shallow waters (<1.5 m, mostly <0.5 m, Fig. 2b).

Study design

To determine the impact of the development of the Marker Wadden on lake Markermeer, we collected samples in the four-meter deep water of the lake surrounding the islands (i.e. the limnetic zone) and in the sheltered conditions of the new islands along the gradual shorelines (i.e. the littoral zone) between 2016 and 2024. The limnetic zone represents the control, pre-restoration condition of the lake, while the littoral zone reflects the treated restored region of the lake. In these zones we determined the maximum primary production rate of the main primary producers and the community composition and biomass of macroinvertebrates species. The organic matter sources and flow to macroinvertebrate consumers were determined using stable isotope analysis on carbon and nitrogen (Post 2002; Middelburg 2014).

Benthic primary producers

To assess maximum primary production rates of periphyton, sediment samples were collected on 9 September 2020 from both the limnetic and littoral zones using a Uwitech gravity corer and a hand corer, respectively (cores diameter 6 cm, n = 7). The top cm of the sediment, containing the active periphyton layer, was carefully subsampled and transferred into airtight incubation chambers filled with site water. Samples were incubated under natural light conditions at the surface to mimic maximum in situ irradiance. From the change in oxygen concentration in the chambers, measured using an Oxy4-optode, oxygen production was calculated (g O_2 m^{-2} d^{-1}). Since macrophytes were not present in the limnetic zone, macrophyte biomass was only sampled in the littoral zone on 17 August 2021. Along two 25 m transects extending from the shoreline to a water depth of 80–100 cm (Fig. 2b), all macrophyte biomass within a 1 m^2 area at each sampling point (n = 40) was collected and stored in plastic bags. The collected plant material, consisting dominantly of *Myriophyllum spicatum* and *Potamogeton* spp., was first air-dried for three days at 20 °C, then dried in an oven at 70 °C for 48 h, after which dry weight (DW) was determined to the nearest milligram.

Benthic macroinvertebrates

The macroinvertebrate community was sampled at 19 limnetic and 11 littoral locations between 20 and 30 August 2024 (Fig. 2a,b). At the littoral zone, sediment was obtained using three cores (ø 6 cm, depth 10 cm) and at the limnetic zone using a Van Veen grab sampler (surface area 14×20 cm, depth 10 cm). Obtained samples were sieved over a 0.5 mm mesh with the retrieved macroinvertebrates stored separately in 70 % ethanol at 5 °C. In November 2024, all invertebrates were taxonomically identified to family-level using a stereomicroscope (Leica MZ FL III) and measured (length) to calculate macrofauna species richness, densities and biomass (dry weight) based on length-mass power regressions at each location (Benke et al. 1999; Méthot et al. 2012; Mährlein et al. 2016; van Leeuwen et al. 2025). Taxa were assigned one of the following functional feeding guilds based on Tachet et al. (2010): Filter feeder, Shredder, Gatherer, Predator, or Grazer if they were a combination of all. This classification is mainly used indicative here and is therefore only visually used as clarification in the figures and not statistically analysed for possible differences among the groups, as most taxa will have a varying diet over the seasons and a diet that consists partly of all kinds of material. However, all have a dominant preference as indicated in the figures.

Organic matter sources and flow to invertebrate consumers

We used stable isotope analysis to determine sources of organic matter and the flow to invertebrates in the littoral and limnetic zone.

To analyse the food web in the limnetic zones, we sampled at 19 different locations in the open water around the Marker Wadden (Fig. 2a,b). We collected sediment (n = 26), macroinvertebrates (n = 34), organic matter samples (n = 3), phytoplankton (n = 52) and zooplankton (n = 3) for stable isotope analyses (Table S1) between 2016 and 2022. Sediment organic matter (SOM) was collected across the lake using an Ekman grab sampler to obtain 50 mL samples of the top sediment (0–2 cm). Macroinvertebrates and organic matter were collected from sediment samples taken using a Van Veen grab (volume 6 L; surface area 0.285 m^2) and sieved over a 1 mm mesh. Phytoplankton and zooplankton were collected by filtering surface water consecutively over two mesh size nets (50 μm Hydrobios phytoplankton net and 335 μm Hydrobios zooplankton net, respectively). Although this size-fractionation method is often used in lake studies (e.g. Tack et al. 2024), it should be noted that phytoplankton could include small zooplankton and suspended matter.

To analyse the food web in the littoral zones of Marker Wadden, we sampled at 18 different locations in the sheltered shore zones of the islands (Fig. 2a,b). We collected sediment (n = 14), macroinvertebrates (n = 108), zooplankton (n = 22), macrophytes (n = 10), periphyton n = 22), filamentous algae (n = 3), and plants on the shoreline growing above the water line (n = 22, Table S1) between 2016 and 2022 (Table S1). Benthic macroinvertebrates and sediment were sampled in 10 to 100 cm deep water by 10-cm taking deep sediment cores (diameter 5 cm), and sieving this over a 0.5 mm mesh sieve to extract macroinvertebrates. Zooplankton was sampled by filtering 10 L of depth-integrated water samples over a 80 um zooplankton net. Submerged macrophytes and filamentous algae were sampled by hand from a boat. Periphyton samples were collected by scraping periphyton from strips placed in the water for six weeks. Shoreline plant species were sampled by clipping leaves from plant species selected based on their abundance close to the waterline, following the assumption that those species growing close to the water line would be most likely to provide plant matter washing into the water. This plant material is further referred to as “shore plant matter’ to reflect that they would represent the more terrestrial source of carbon for aquatic organisms. Sampled species included *Phragmites australis, Typha latifolia, Epilobium hirsutum, Tephroseris palustris, Alisma plantago-aquatica* and *Rumex maritimus.*

Both the limnetic and littoral stable isotope samples were collected in 15 mL or 50 mL plastic tubes and stored in water at 4 °C within 24 h. Macroinvertebrates were identified and sorted at family level, frozen to −18 °C, and then freeze-dried. Homogenization and powdering of the macroinvertebrate samples was done by hand, using a small metal stick that fitted into the Eppendorf tubes. Most samples were combinations of multiple individuals from the same species and locations (e.g. multiple gammarids) to obtain sufficient material for the analyses. Samples of terrestrial plants and macrophytes were homogenized by using a mortar and pestle (when the plant material was very stiff or fibrous, liquid nitrogen was added to speed up the grinding process). To remove non-dietary carbon, sediment samples were put into porcelain cups and acidified with 4 M HCl until CO_2 release was no longer visible, to remove carbonates that may distort the carbon signals (Leng & Lewis 2017). The samples were left on a heating plate set to 80 °C to dry overnight in a fume hood. Then, the sandy sediment samples were sieved over a 1.4 mm mesh to remove the relatively large pebbles that were not suitable for the stable isotope analysis. After sieving, the samples were left to dry in a fume hood for three more nights.

From each stable isotope sample, we weighed between 0.3 and 30 mg of dried material (depending on the type) and folded this material into tin weighing cups that were placed into 96-wells plates. Carbon and nitrogen content and stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of the samples were assessed with an elemental analyser (Flash 2000, Thermo) coupled via Conflo IV to an isotope ratio mass spectrometer (IRMS, Thermo Delta XP advantage). The samples were measured against reference standards of carbon (Caffeine $\delta^{13}C$ or Vienna PeeDee

Belemnite, internal precisions respectively 0.20‰ and 0.03‰) and nitrogen (Wenen N2C6 δ^{15}N or atmospheric N_2, internal precision respectively 0.14‰ and 0.10‰) as described in Werner and Brand (2001). The δ^{13}C and δ^{15}N ratios are expressed in parts per thousand (‰) deviating from the reference standards: $\delta^{13}C = (R_{sample}/R_{standard} - 1) * 1000$, where R is the isotope ratio $^{13}C/^{12}C$ in the sample and in the standard, respectively. Negative values indicate less heavy isotopes in the sample compared to standards (Fry, 2006).

Data analyses

Stable isotope values of primary producers, primary consumers and SOM were plotted in δ^{13}C-C:N and δ^{13}C-δ^{15}N coordinate planes for direct comparison of energy fluxes. Data were analysed with adjustments of the macroinvertebrate community isotopic values for Trophic Discrimination Factors (TDFs). We applied correction factors of +1.0‰ for δ^{13}C and +3.4‰ for δ^{15}N, following recommendations by Post (2002) and McCutchan et al. (2003).

Differences in mean and variances of carbon isotope values between macrofauna with different origins were tested using Linear Mixed-Effects models with the δ^{13}C values as dependent variable, habitat as fixed factor (littoral or limnetic zone) and year was included as random intercept to account for non-independence of observations across years. One model was constructed for each feeding type, except for Grazers because these were only found in the littoral habitats. The model for Predators could not include year as random factor, because too few Predators were found in the limnetic zone. For Filter feeders, Gatherers, Predators and Shredders, we tested for statistically significant differences in mean values between levels of habitat (littoral or limnetic) with order-independent Type III ANOVAs. To assess whether allowing for heteroscedasticity among habitat types improved model fit, we fitted an alternative mixed-effects model that allowed the residual variance to differ by habitat using a varIdent structure. This model specified distinct variance parameters for each habitat category while keeping the same fixed and random effects structure as the baseline model. Model performance between the homoscedastic and heteroscedastic models was compared using likelihood-ratio tests. For all feeding types, we assessed spatial dependence in model residuals using Moran's I, and accounted for positive spatial autocorrelation in the model for the Gatherers by fitting a spatial LME model that incorporated an exponential spatial correlation structure (corExp) based on the latitude and longitude of the sampling locations. Models were constructed using the nlme package in R (Pinheiro et al. 2021).

Macroinvertebrate δ^{13}C and δ^{15}N data were compared between the littoral and limnetic zones for isotopic niche width, total convex hull area, convex hull perimeter, nearest-neighbor distance and standard ellipse area (corrected for sample sizes) using package SIBER in R (Jackson et al. 2011). All statistical analyses were performed with R version 4.5.1 for statistics (R Core Team 2025).

Results

Benthic primary producers

The maximum potential productivity (i.e., at surface light intensity) of the periphyton in the littoral zone (mean ± SD, 8.2 ± 1.2 g O_2 m^{-2} d^{-1}) almost fourfold exceeded that of the periphyton in the limnetic zone (2.7 ± 0.4 g O_2 m^{-2} d^{-1}; Welch's two sample *t*-test, $t = -11.8$, df = 7.72, $P < 0.001$; Supporting Information Fig. S1a). An important corresponding variable to this pattern was the increase of light availability over the water depth gradient, as Photosynthetically Active Radiation (PAR) (Fig. 2c). Submerged macrophytes appeared in the constructed littoral zones (Fig. S1b), with plant biomass exceeded 200 g DW m^{-2} during the growing season five years after the start of the restoration project (August 2021).

Benthic macroinvertebrates

Dry biomass of the benthic macroinvertebrate community in the littoral zone did not statistically differ from dry biomass in the limnetic zone (mean ± SE, 366 ± 81 g m^{-2} and 171 ± 17 g m^{-2}, respectively, Welch Two Sample *t*-test on log10(x + 0.001)-transformed values, $t = -1.00$, $df = 21.5$, $P = 0.33$, Fig. 3a). The macroinvertebrate community composition in the limnetic zone had a low diversity and the functional feeding guilds of the community consisted mainly of Gatherers (48 % of individuals; Polychaeta, Chironomidae larvae) and Filter feeders (35 %; Dreissenidae) with some Shredders and Predators present (7 %, Fig. 3b). In the littoral zone, the macroinvertebrate community was still dominated by Gatherers (56 %; Chironomidae larvae, Corixidae), but the proportion of Filter feeders was much smaller in this zone (5 %). Instead, the Shredders and Predators like Amphipoda (Gammaridae) made up a large proportion (24 %), while here also Grazers were present like Gastropoda (15 %; Physidae, Lymnaeidae, Hydrobiidae) (Fig. 3b).

Organic matter sources and flow to macroinvertebrate consumers

The molar C:N ratios and stable isotope signatures of carbon and nitrogen differed among the four groups of primary producers present in the study system: terrestrial vegetation on the shorelines, submerged macrophytes, periphyton and phytoplankton (Fig. S2). The molar ratio of C:N varied between 10 for phytoplankton up to around 30 for shore plants and periphyton (Fig. 4a). The variation in C:N ratios was relatively large for these latter two groups: δ^{13}C values were the most depleted for phytoplankton (−21.8‰ ± 4.5 SD) and shore plants (−29.4‰ ± 1.3 SD), and the most enriched for the benthic primary

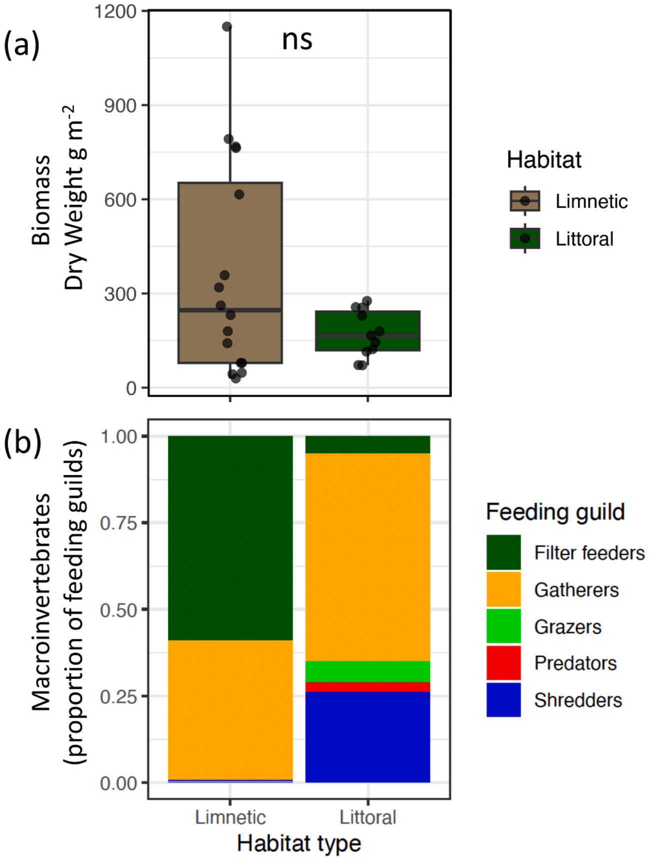

Fig. 3. Macroinvertebrate (**a**) dry mass in g m^{-2}, and (**b**) community composition (% density) divided into functional feeding guilds, sampled in the original limnetic zone (close to the constructed islands in the lake, $n = 18$) and at the new littoral zones (along the shoreline islands, $n = 18$) in August 2024.

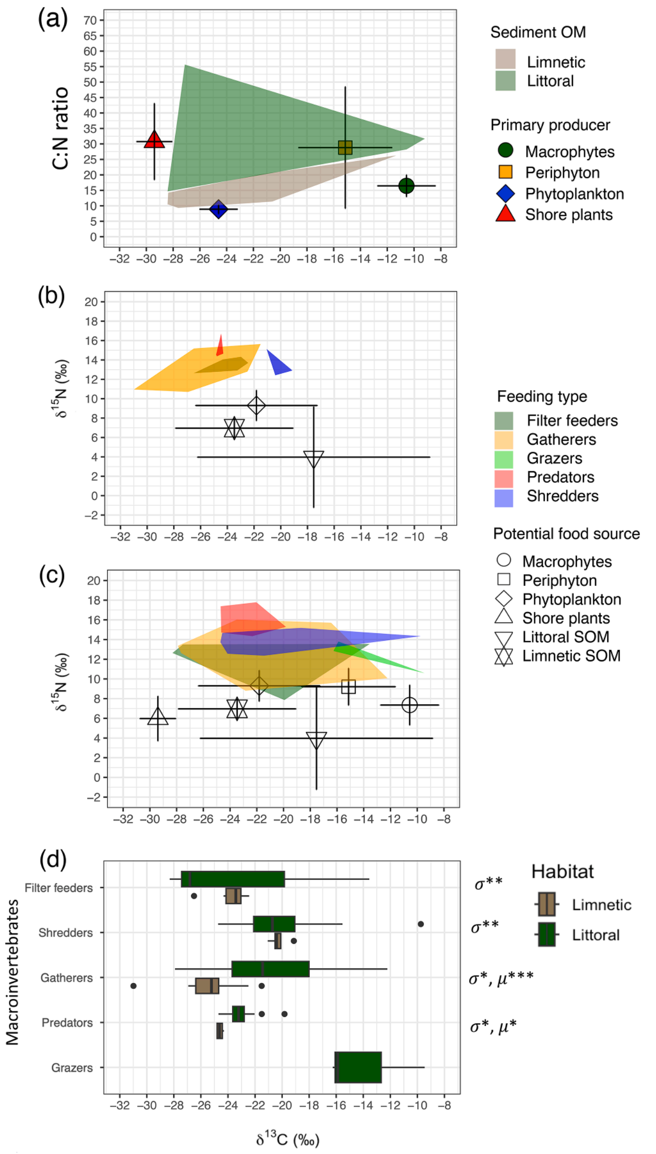

Fig. 4. (**a**) Carbon stable isotope values ($\delta^{13}C$) in relation to Carbon:Nitrogen ratios in Lake Markermeer and Marker Wadden for the four types of primary producers depicted as means (±SD) and values for Sediment Organic Matter (SOM) in the original limnetic ($n = 26$) and the newly sheltered shoreline islands ($n = 19$). (**b**) Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of macroinvertebrates (polygons coloured by feeding guilds) and their potential food sources (grey symbols with error bars) for the original limnetic open water habitat, and (**c**) the same for the new littoral habitat. (**d**) Carbon isotope signatures ($\delta^{13}C$) of macroinvertebrates with different feeding guilds in the limnetic and the littoral zones. Results of Linear Mixed-effects models are depicted for differences in variances and means between the two habitat types are indicated with asterisks and their respective symbols (details in Table 1).

producers (submerged macrophytes −10.5‰ ± 2.2 SD and periphyton −15.1‰ ± 3.5 SD; Fig. 4a). Nitrogen isotope values were positive for all primary producers, with $\delta^{15}N$ values ranging from around 5‰ in shore plants to over 10‰ in periphyton and phytoplankton (Fig. 4b).

We then used these signatures to assess the flow of organic matter from the various primary producers to both the sediment and macroinvertebrate consumers. Overall, the C:N ratios of the limnetic sediment organic matter (SOM) were higher compared to the littoral SOM, with relatively comparable ranges in $\delta^{13}C$ values for both SOM. The planes covered by the SOM; indicated that at the limnetic zone the main source of OM was phytoplankton derived carbon (Fig. 4a). In the littoral zones, the SOM plane was much wider and overlapped with other OM sources including benthic primary producers and shore plants.

Organic matter flows to the macroinvertebrate consumers were similarly more limited in the limnetic zones (Fig. 4b and Fig. S3a) compared to the more diversified OM flows in the littoral zones (Fig. 4c and Fig S3b). This is both due to the increased variation within the functional feeding guilds and taxonomic orders present in both zones (i.e. larger planes covered by each feeding guild) as well as additional feeding guilds and taxonomic orders present in the littoral zone (e.g. Grazers). Overall, the macroinvertebrate feeding guilds responded in three different ways on the constructed littoral zone compared to the original limnetic zone: 1) a broader use of available OM sources by Filter feeders, Gatherers, Predators and Shredders (Table 1); 2) a shift towards feeding on more benthic OM sources by Gatherers (difference in mean $\delta^{13}C = 4.6‰$) and Predators (difference in mean $\delta^{13}C = 1.5‰$, Table 1); and 3) the arrival of Grazers with a predominantly benthic OM signature (mean $\delta^{13}C$ of −14.9‰; Fig. 4d).

Isotopic metrics revealed that macroinvertebrates in the littoral zone had a larger isotopic niche than macroinvertebrates in the limnetic zone (Table 2). Across all species, the total convex hull area of the nitrogen and carbon isotopes was about twice as high in the littoral zones as compared with the limnetic zone, and the standard ellipse area (corrected for sample sizes, SEAc) was also higher. This indicates a broader trophic niche and more diverse diet in the littoral zones. In accordance, the mean nearest-neighbor distance (NND) and its standard deviation (SDNND) indicated that in the new littoral zone species were more clustered together, suggesting higher densities and trophic redundancy with more species occupying similar ecological niches than in the limnetic zones. This was across all species, but also within taxonomic groups: for Bivalvia, Oligochaeta and Polychaeta $\delta^{13}C$ variances were up to 10-fold higher in the littoral zone, and within families of Gammaridae and Dreissenidae littoral zone variances were respectively 9.37 and 40.17, compared to 0.50 and 0.61 in the limnetic zones.

Discussion

Human-induced loss of habitat heterogeneity in ecosystems is often followed by a loss of productivity, food sources and associated biodiversity (Agra et al. 2024). This study shows that by locally increasing abiotic habitat heterogeneity in a degraded homogeneous lake, the aquatic food web can be stimulated. The creation of hundreds of hectares of new shallow sheltered waters and the softening of shorelines was found to reinstate previously lost connections and energy fluxes among terrestrial, pelagic and benthic habitats. Shallower water depths combined with lower sediment resuspension rates increased light availability for benthic primary producers (periphyton and macrophytes), and gradual vegetated shorelines facilitated the influx of terrestrial material into the aquatic ecosystem (Fig. 1). These more diverse sources of organic matter that became available to the aquatic food web suggest that a more balanced and natural autotrophic structure (i.e. the balance between pelagic, benthic and terrestrial primary production) was formed in the lake (Francis et al. 2011; Vadeboncoeur et al. 2011; Vander Zanden & Vadeboncoeur 2020), in a time span of less than eight years. Macroinvertebrate primary consumers benefitted from the diversification of primary producers, and can in turn be expected to provide additional food sources for higher trophic levels such as fish and birds (Jin et al. 2024). This study therefore mechanistically explains the previously documented positive effects of the abiotic changes on the higher trophic levels of the food web, particularly fish and birds (Jin et al. 2022, 2023; van Leeuwen et al. 2023; de Leeuw et al. 2024; van der Winden et al. 2024).

Marker Wadden represents an example of a large-scale habitat restoration project in which the diversity of basal resources increases through diversification of sediment structures and water depths, followed by increased complexity of the basal food web. This type of effects can also be expected in other ecosystems in response to large scale

Table 1

Results of Linear Mixed-Effects models testing for differences in means and variances of δ^{13}C values between habitat types for each of the feeding types. Indicated are the effects of the fixed factor habitat with degrees of freedom, F-values and p-values for differences in means among habitat types, and the results of Likelihood Ratio Tests (LRT) with associated p-values testing for differences in variances among habitat types.

Feeding type	LME fixed effect (habitat)	df (num, den)	F	P-value	Differences in variance test (LRT)	Variance P-value
Filter feeders	No effect	1, 9	0.14	0.71	8.45	**<0.01**
Gatherers*	Significant effect	1, 70	21.68	**<0.0001**	7.56	**<0.01**
Predators**	Significant effect	1, 0	6.46	**0.02**	5.81	**0.02**
Shredders	No effect	1, 1	0.18	0.74	5.31	**0.02**
Grazers	Only present in littoral habitat					

* Model corrected for spatial autocorrelation after significant Moran's I test (Moran's $I = 0.64$, $p < 0.001$).

** Model did not include year as random intercept because of too few observations of predators in the limnetic zone.

Table 2

Results of stable isotope basian ellipses analysis in R (SIBER), comparing limnetic and littoral habitats.

Metric Description	Limnetic	Littoral
Range of δ^{15}N values	6.01	9.93
Range of δ^{13}C values	11.85	18.84
Total convex hull area (TA)	37.33	122.92
Convex hull perimeter (CD)	2.16	3.5
Mean nearest-neighbor distance (NND)	0.7	0.56
Standard deviation of nearest-neighbor distances (SDNND)	0.75	0.59
Small-sample corrected standard ellipse area (SEAc)	9.43	20.15

abiotic changes, based on classical heterogeneity-richness relationships and an increase in available niche space (Stein et al. 2014). However, the precise rate of the response at the food web level likely depends strongly on the environmental conditions in target habitats, such as mean temperature, duration of the growing season, availability of nutrients in the sediment and water, hydrology and disturbances. In the temperate region of our study site, wetland vegetation succession typically requires multiple years (Alderson et al. 2025) despite high sediment nutrient levels (van Leeuwen et al. 2023). Although submerged macrophyte development can occur fast under suitable conditions (Bakker et al. 2013) their establishment is sensitive to disturbances of sediment by wind (Jin et al. 2022). The long-term stability and success of the Marker Wadden project – and other large-scale restoration projects in comparable lakes elsewhere – will therefore depend on the interplay between vegetation succession and sedimentation on the one hand versus disturbances by storms and erosion on the other hand.

Changes in the autotrophic structure

The autotrophic structure of a lake can shift seasonally, spatially or in response to changes such as arrival of invasive species (Rautio et al. 2011; Brothers et al. 2013; Mayen et al. 2025). The autotrophic structure can also vary among lotic and lentic systems (Leal et al. 2023) and among lakes (Wetzel 1990), with larger and more circular lakes with relatively less physical space for shorelines relying relatively more on pelagic primary production, shallower lakes on benthic production and those with extensive shorelines on terrestrial production (Dolson et al. 2009; Francis et al. 2011). Here, we showed that shifts in autotrophic structure are also reversible if human engineering activities have altered the natural balance.

Within only a few years after its formation, the created sheltered shallow waters boosted periphyton and macrophyte production, thereby supporting the base of the food web (Fig. 1). Newly created shelter was a strong driver of this, as previous work has shown that artificially created shelter in enclosures resulted into immediate colonization by submerged macrophytes (Jin et al. 2022) followed in subsequent years by macrophytes establishment in all shallow sheltered waters of Marker Wadden (Scirpus Ecologisch Advies 2020). Quantification of biomass per m^2 in 2021 revealed high densities of benthic primary production (Fig. S4), that strongly expanded in subsequent years (pers. comm. CvL).

This high potential for benthic primary production in response to abiotic changes in Lake Markermeer (Fig. S1) may be related to its eutrophic history. Lake Markermeer has long been a eutrophic lake due to wastewater disposal and high nutrient fluxes from the Rhine River, with only a reduced nutrient influx in the last few decades (Van Riel et al. 2019). Nutrient concentrations in the Marker Wadden sediments were ~3.88 mg/kg for nitrogen and ~0.75 mg/kg for phosphorous at a pH of between 8 and 9 in 2020 (van Leeuwen et al. 2023). These nutrients are normally locked in lake Markermeer's sediment in the dark by binding to available iron (Brinkmann et al. 2019), but in the new littoral zones the iron is oxidized and the phosphorous becomes bioavailable. The nutrients are taken up by macrophytes and benthic periphyton and further fuel the food web bottom-up. Under the new light conditions around the Marker Wadden, benthic primary producers were stimulated to grow and take up and release nutrients to the more productive food web (van Leeuwen et al. 2023). These released nutrients are re-entering the aquatic community, and – in the form of wreck washing ashore – may also be entering the terrestrial ecosystem (Figure S3, showing macrophyte wreck washed on the shorelines). The resulting broader basis of the food web explain the productive and resilient lake ecosystem at the local scale (van Leeuwen et al. 2023).

Temporal response to restoration

Both autochthonous and allochthonous processes contributed to the recoupling of pelagic, benthic and terrestrial habitats in our study, but the autochthonous increase of benthic primary production seemed to provide a more direct stimulation than the allochthonous input for the macroinvertebrate community. Carbon isotope ratios of two functional feeding guilds indicated that these species had ingested OM from shore plants, while five functional feeding guilds had partly or solely ingested benthic OM. These observations correspond to the findings in boreal peatlands (Ferguson et al. 2021) where organic matter from autochthonous resources contributes most to the diet of secondary producers. This difference may be related to the higher quality (lower C:N ratio, see also Fig. 4a) of benthic and pelagic OM as food for macroinvertebrates than terrestrial OM with relatively more carbon, which is required to build structural plant components (Leal et al. 2023). In lakes with low to intermediate productivity, the contribution of autochthonous resources (benthic and pelagic algae) to consumers in higher levels of the food web is generally much higher than the contribution of allochthonous resources, such as terrestrial carbon (Brett et al. 2017). This phenomenon does not only apply to freshwater systems; it was found that benthic primary production plays a key role in stimulating the food web in many coastal ecosystems worldwide (Christianen et al., 2017), with trophic transfer to higher trophic levels including fish (Maathuis et al. 2024).

Since the Marker Wadden were created in 2016 and now monitored only during the first eight years, their development should be interpreted as a response of a pioneer system. As tree growth and shoreline development continue over time, terrestrial influx may become more important as well (Leal et al. 2023), although such a long-term impact on the food web at the lake scale should still be assessed. The rapid discovery of the islands by many fish and bird species and the rapid diversification of the primary producers already suggests that a large-scale impact can be expected, but locally produced organic matter may also be directly re-consumed by local biota. Next monitoring steps therefore include investigating which higher trophic levels may profit specifically from such changes in available gradual shorelines (Dolson et al. 2009; Stiling et al. 2023), whether the realized 16 % increase in soft shoreline habitat in the lake is sufficient to recouple littoral and pelagic habitats in relation to bathymetry of the shorelines (Dolson et al. 2009) and how far from the constructed littoral zones OM may be detectable in the large lake ecosystem (Godshalk and Wetzel 1984). The processes underlying habitat coupling seem sensitive to shoreline modifications, land use change, water level fluctuations and other human impacts. This emphasizes the importance of maturity of an ecosystem since the last disturbance, either by humans or potentially by e.g. climatic events such as floodings or droughts, that can cause resets of systems (Wernberg et al. 2013; Datry et al. 2017; Jabbari et al. 2021).

Forward-looking restoration

The rapid ecological development of the Marker Wadden restoration project is an example of a new type of thinking about ecosystem restoration. We have here shown mechanistically how the increase of abiotic heterogeneity in a homogenous habitat can stimulate a degraded food web via allowing natural ecological processes to take place. However, the former abiotic conditions and species richness of the marine estuary that was formerly here did not return. By stimulating local productivity, diversification of food sources, and enhanced exchange between terrestrial, benthic and pelagic habitats, the food web in the new freshwater setting is broadened and more robust to support higher trophic levels like fish and birds. The species richness and productivity of the modified ecosystem increased, while ecosystem services such as water safety and drinking water provisioning were maintained (van Leeuwen et al. 2021). This makes this project an example of a forward-looking restoration process (van Leeuwen et al. 2021). This new restoration approach offers opportunities beyond wetland ecosystems and aquatic food webs, if we embrace that restoration outcomes can be mechanistically understood and predicted (i.e. this study), but are less directly predictable (at the species level) than classical restoration (Higgs et al. 2014).

CRediT authorship contribution statement

C.H.A. van Leeuwen: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **H.G. van der Geest:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **J. Bom:** Writing – review & editing, Investigation, Formal analysis, Data curation. **J.J. de Leeuw:** Writing – review & editing, Investigation, Data curation. **L.F.J. Tack:** Writing – review & editing, Investigation, Data curation. **G.H. van Beilen:** Writing – review & editing, Investigation, Data curation. **J.A. Vonk:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank many students, collaborators and technicians for inspiring discussions and support over the last years, and the Dutch Society for Nature Conservation (Natuurmonumenten) and its volunteers for their facilitation of research on the Marker Wadden.

Supplementary materials

Supplementary material and data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2026.01.003.

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