Basal food sources for the invertebrate food web in nutrient poor and nutrient enriched raised bog pools

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Intact raised bog pools are extremely nutrient-poor and represent a harsh environment for invertebrates. In the Netherlands, nutrient availability in raised bog pools is increased, due to atmospheric nitrogen and sulphur deposition, and the macroinvertebrate species composition is altered. This paper assesses whether the increased nutrient availability has changed the importance of food sources at the basis of the invertebrate food web in bog pools, such as algae, *Sphagnum* or dead organic matter. To this end, stable isotope ratios of carbon and nitrogen of basal food sources and aquatic invertebrates were compared between nine bog pools, which differ in nutrient availability, in Estonia and the Netherlands. For most invertebrates the trophic levels in the food web inferred from their isotope ratios corresponded with common ecological knowledge. Isotope ratios of specimens of large mobile bugs and beetles differed strongly, most likely because they foraged in different water bodies. For a part of the invertebrate community trophic relations could not be inferred from the measured food sources. One or more basal food sources with a ratio $\delta^{13}C < 30‰$ still need to be identified. This unidentified food source becomes more important with decreasing nutrient availability. We suggest that only in the most nutrient enriched raised bog pools the quality of dead organic matter and/or the abundance and quality of algae are sufficient to support the whole invertebrate community.

Keywords: food web, stable isotopes, carbon source, eutrophication, raised bog

The aquatic macroinvertebrate assemblages of the most nutrient poor raised bog pools in Estonia are not found in Dutch raised bog pools (Van Duinen *et al.*

2002). The macroinvertebrate assemblage of Dutch bog pools is dominated by species whose occurrence in intact Estonian raised bogs is limited to water bodies with a naturally higher nutrient availability, such as transitional mires and bog brooklets. This difference in the species assemblage between Estonian and Dutch raised bog pools was found for different taxonomic groups and different trophic levels: oligochaetes and chironomids feeding on detritus and algae, omnivorous bugs and carnivorous beetles and dragonfly larvae (Van Duinen *et al.* 2004, 2006).

Intact raised bogs are extremely nutrient-poor while also the nutritional value of bog plant material is extremely low. Western European raised bogs are threatened by increased deposition of atmospheric nitrogen and sulphur compounds (Roelofs 1986, Lamers *et al.* 2000). Increased N deposition in raised bogs leads (i) to a higher N availability in the surface and interstitial water, (ii) to a higher cover of vascular plants such as *Molinia caerulea* and *Betula* spp. (Limpens *et al.* 2003a, Tomassen *et al.* 2003) and (iii) to an elevated N content of *Sphagnum* mosses (Lamers *et al.* 2000, Limpens *et al.* 2003a). As a result, both the input and nutritional quality of dead organic material in bog pools are enhanced. Consequently, the decomposition rate and nutritional value of dead organic matter might increase (Lamers *et al.* 2000). SO_4 can further increase the anaerobic oxidation of organic matter leading to an increased release of both NH_4 and PO_4 in bog water bodies (Lamers *et al.* 1998). Increased availability of N and P leads also to a higher growth rate and nutrient content of algae (Gulati & DeMott 1997, Limpens *et al.* 2003b). These changes in quantity and quality of basal food sources such as algae, mosses, vascular plants and dead organic matter likely affect their importance in the invertebrate food web in raised bog pools.

This paper addresses the question if and how the basal food sources in the invertebrate food web differ between intact and nutrient enriched raised bog pools. For this purpose, the stable isotope ratios of carbon and nitrogen in dead organic matter, living vascular plants, mosses, algae and aquatic micro- and macroinvertebrates were compared between several bog pools in Estonia and the Netherlands, which differ in nutrient availability.

MATERIAL AND METHODS

Three bog pools were sampled in Nigula bog, Southwest Estonia, between 9 and 23 September 2002. In the Netherlands, six peat cuttings and inundated peat extraction fields were sampled in five raised bog remnants in total between 7 October and 15 November 2002. At each site surface water and sediment pore water samples were collected at least once in spring and once in autumn in the period 1998-2002 (Table 1). For further details about water quality analyses see Van Duinen *et al.* (2003, 2006).

At all sampling sites plants (filamentous algae, mosses and vascular plants) and aquatic macroinvertebrates were collected. Settled dead organic matter was

Table 1. pH and concentrations of o-PO_4 and NO_3+NH_4 (µmol/l) of surface water and sediment pore water at the nine sampling sites (mean ± standard deviation).

	Surface water			Sediment pore water		
Site	pH	o-PO_4	NO_3+NH_4	pH	o-PO_4	NO_3+NH_4
Estonia						
Nigula 1	4.2±0.3	0.2±0.1	13±14	4.9±0.2	0.2±0.1	5.4±4.0
Nigula 2	4.0±0.0	0.1±0.1	12±5.6	4.8±0.7	0.2±0.1	15±16
Nigula 3	3.9±0.1	0.3±0.0	11±9.0	4.5±0.2	0.2±0.1	21±14
The Netherlands						
Haaksbergerveen 1	4.2±0.2	0.8±0.4	14±12	4.8±0.5	1.3±1.2	46±21
Haaksbergerveen 2	4.2±0.1	2.2±2.8	13±7.4	5.5±0.5	1.7±0.5	40±14
Korenburgerveen	3.7±0.1	0.9±0.2	11±4.1	5.1±0.9	0.8±0.1	21±11
Reigerplas	4.2±0.5	0.4±0.3	8.3±2.8	5.0±0.0	3.2±2.3	110±131
Mariapeel	4.0±0.1	3.4±17	23±21	5.0±0.4	18±19	201±117
Bargerveen	3.8±0.1	5.6±8.2	20±16	4.5±0.5	82±102	213±219

collected from the peat bottom by means of a plankton net with mesh size 45 µm. Zooplankton was collected from the open water by means of this plankton net and light traps. It was not possible to obtain clean samples of phytoplankton and suspended particulate organic matter. Gut contents were not removed from invertebrates. The collected material was sorted, washed with demineralised water and kept in a fridge until identification. Identified material was dried for 24 hours at 70°C and subsequently ground, using liquid nitrogen. Large macroinvertebrates were analysed individually. Carbon and nitrogen isotopic composition was determined. Average reproducibilities of duplo and triplo measurements were <0.2‰. Stable isotope data are presented as the relative difference between the ratios of the sample and the standards, using the following formula:

$$\delta R = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $\delta^{13}C$ or $\delta^{15}N$ is the per mille (‰) deviation of the sample from their isotope standards, that are PeeDee belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

RESULTS AND DISCUSSION

Figure 1 shows a scatter plot of $\delta^{15}N$ against $\delta^{13}C$ of dead organic matter, plants and aquatic invertebrates of the intact raised bog pool Nigula 1. Different invertebrate species collected within one bog pool differ in their $\delta^{13}C$, indicating differential use of carbon sources, and in their $\delta^{15}N$, indicating the presence of various trophic levels. The highest $\delta^{15}N$, in the range of 1.2 to 10.3‰, was found for the heteropterans *Notonecta glauca*, *Nepa cinerea* and *Ranatra linearis*, the water spider *Argyroneta aquatica*, and the coleopterans *Dytiscus dimidiatus*, *Acilius canaliculatus* and *Acilius sulcatus*, which can be considered as top-predators. The $\delta^{15}N$ of other heteropteran species and larvae of chironomids, dragonflies, damselflies and caddis flies were between 2.8 and -0.3‰. The invertebrates with the lowest $\delta^{15}N$ were zooplankton (dominated by the microcrustaceans *Bosmina* sp., *Chydorus sphaericus* and copepodites) and *Psectrocladius* larvae (Chironomidae). These two groups of invertebrates can be considered as primary consumers, in addition to several omnivorous bugs and caddis fly larvae. For most invertebrate groups or species the trophic levels in the food web inferred from their $\delta^{15}N$ correspond with available literature data.

Specimens of *Acilius canaliculatus*, *Acilius sulcatus* and *Notonecta glauca* differed strongly in isotopic signature for both C and N (Fig. 1), indicating use of prey items differing considerably in their isotopic signature. As these *Notonecta* and *Acilius* species are mobile, immigration from other pools with other isotopic signatures of basal resources most likely explains the high intraspecific variability.

There was a discrepancy between the $\delta^{13}C$ of sampled food sources and the $\delta^{13}C$ of the sampled invertebrates when an enrichment (less negative) of 0 to 1‰ for $\delta^{13}C$ between trophic levels (McCutchan *et al.* 2003) is assumed. For example, in pool Nigula 1, $\delta^{13}C$ of dead organic matter and living plants ranged from -28.3 to -24.3‰, whereas $\delta^{13}C$ of invertebrates ranged from -34.8 to -24.2‰. What is the basal food source for the invertebrates with a $\delta^{13}C < -28.3$‰? Although consumers can be depleted (more negative) in $\delta^{13}C$ relative to their food sources by

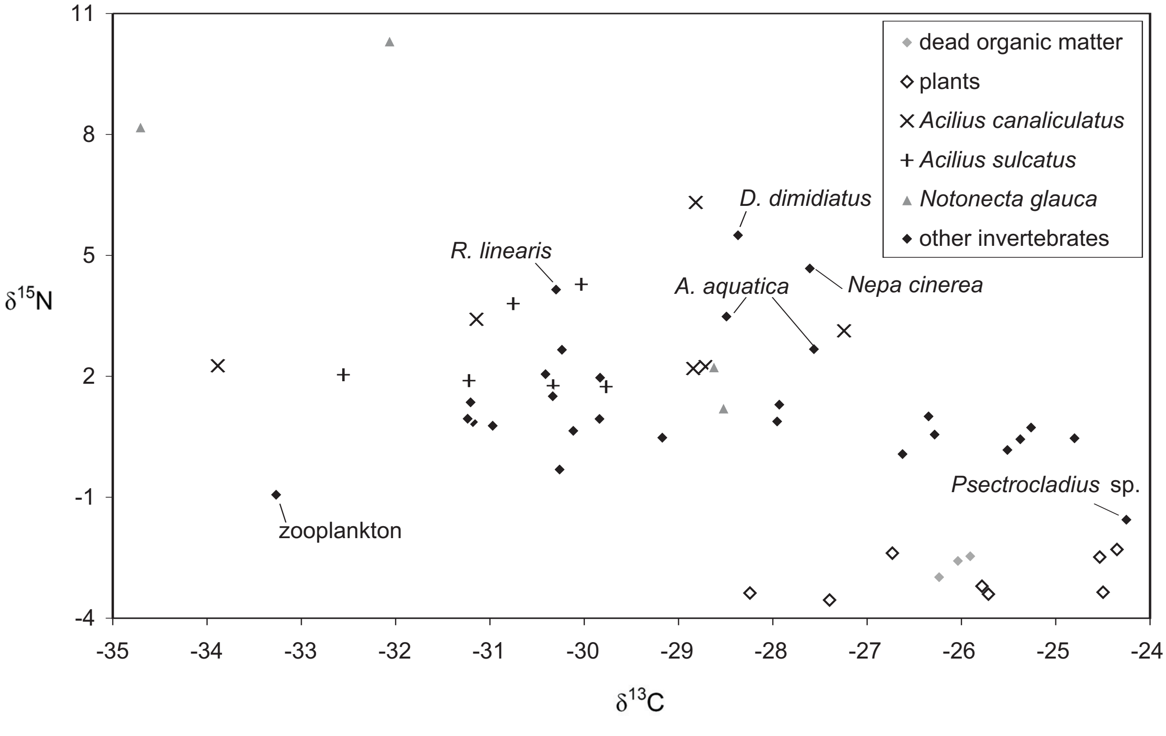

Figure 1. Scatter plot of $\delta^{15}N$ against $\delta^{13}C$ of dead organic matter, plants (vascular plants, mosses and filamentous algae) and aquatic invertebrates of the intact raised bog pool Nigula 1. Invertebrate species mentioned in the text are indicated.

more than 2‰ (McCutchan *et al.* 2003), this cannot account for (all) the large differences between the δ^{13}C of invertebrates and dead organic matter or living plants. The difference between the average δ^{13}C of dead organic matter and living plants and the average δ^{13}C of the invertebrates (hereafter termed average trophic shift) was not consistent for all sampling sites. For the two most nutrient rich sampling sites in Bargerveen and Mariapeel all collected fauna species appeared to be similar or enriched in δ^{13}C compared to dead organic matter and living plants (data not shown). The average trophic shift strongly and positively correlated to nutrient concentrations of surface water and sediment pore water (Fig. 2; $p < 0.025$ for surface water and $p < 0.001$ for sediment pore water).

Different explanations can be given for the observed discrepancy between the δ^{13}C of sampled food sources and the δ^{13}C of the sampled invertebrates. First, the dead organic matter consists of a mixture of dead organic matter from various vascular plants, mosses and animals, as well as algae and attached bacteria, fungi and microinvertebrates. Therefore, the measured δ^{13}C of dead organic matter is a weighted average of its various components. Components without nutritional value for detritivores constitute the major part of the biomass and the δ^{13}C of these components will correspond closely to the δ^{13}C measured for dead organic

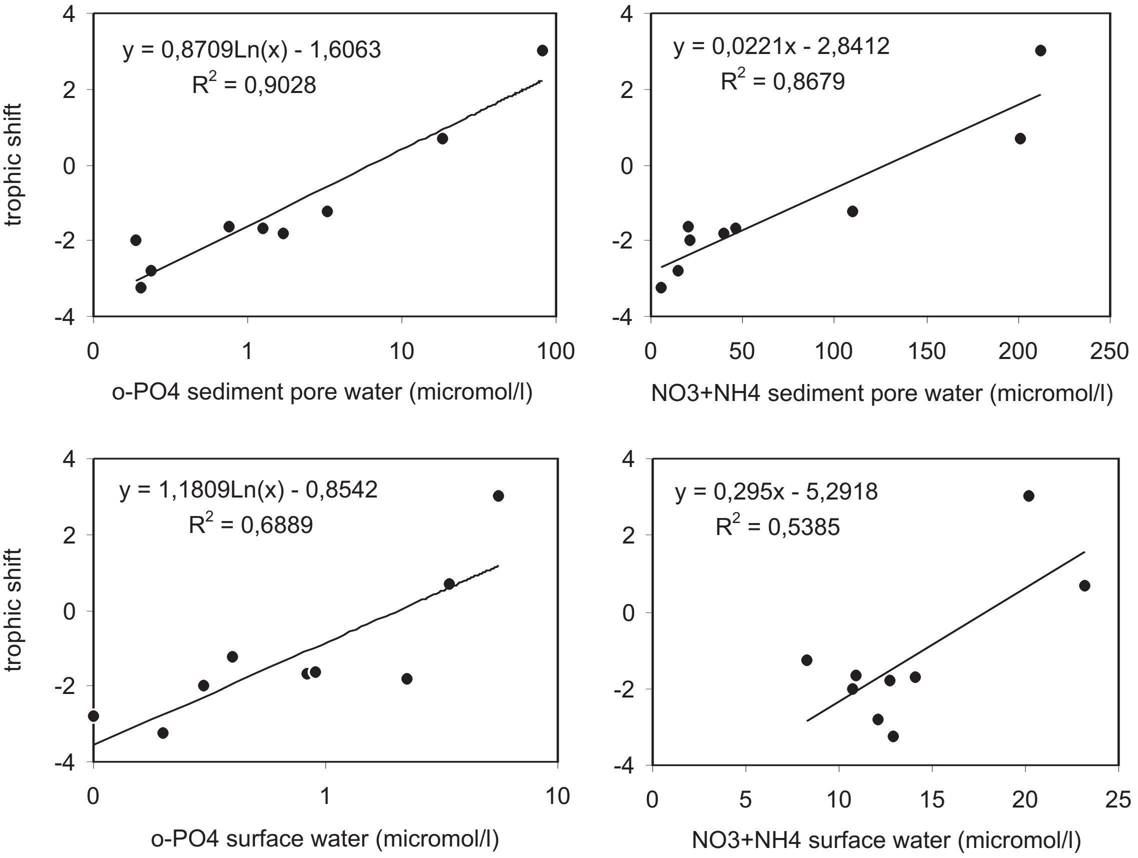

Figure 2. Relationship between the o-PO$_4$ and NO$_3$+NH$_4$ concentrations in surface water and sediment pore water and the average trophic shift (difference between the average δ^{13}C of dead organic matter and living plants and the average δ^{13}C of the invertebrates) for the nine sampling sites.

matter. Conversely, the $\delta^{13}C$ of digestible components, like attached algae, bacteria and fungi, will deviate most from the $\delta^{13}C$ measured for dead organic matter. A $\delta^{13}C$ below -30‰ of these digestible components could explain the observed trophic shift. The $\delta^{13}C$ of the living filamentous algae sampled at all nine sampling sites ranged from -17 to -31‰ (data not shown). If algal species with a $\delta^{13}C$ lower than -30‰ are present at the sampling sites, they could account for the $\delta^{13}C$ of invertebrates lower than -28.3‰. The $\delta^{13}C$ of particulate organic matter (POM) in fresh water ranges between -20 and -35‰ (Del Giorgio & France 1996), although it must be noted that POM is also a mixture of phytoplankton, detritus and attached microbes. The mean difference in $\delta^{13}C$ between macrozooplankton and POM or microplankton in lakes is -2.7‰, due to selective feeding on isotopically light components of POM (Del Giorgio & France 1996, Grey *et al.* 2000). Methanotrophic and chemoautotrophic bacteria are known to have a $\delta^{13}C < -40$‰ and are assimilated by *e.g.* chironomid larvae (Grey *et al.* 2004, Kiyashko 2004, Grey & Deines 2005).

Second, allochthonous food sources could be important (*e.g.*, Grey *et al.* 2000). In the case of the pools sampled in Nigula bog, these allochthonous food sources could be pollen, seeds or leaves of *Betula* and *Pinus* trees, that are scattered in the surrounding bog, and terrestrial insects, for example ants and butterflies, falling and drowning in the pool. The stable isotope signatures of these terrestrial insects have still to be measured. The $\delta^{13}C$ of *Betula* leaves collected at four Dutch sampling sites were between -28.8 and -30.1‰ and the $\delta^{13}C$ of *Betula* seeds was -26.3‰ at one site.

Although the above explanations may explain the negative average trophic shift in bog pools with low nutrient concentrations, it does not explain the absence of a negative average trophic shift in bog pools with high nutrient concentrations. In a study on lake zooplankton, Grey *et al.* (2000) concluded that the relative importance of allochthonous sources of organic carbon decreases with increasing lake trophy. Alternatively, in oligotrophic lakes in which phytoplankton production is limited, zooplankton diets are supported by planktonic heterotrophs and detritus via the microbial pathway (Hessen *et al.* 1990; Jones 1992). We suggest that only in the most nutrient enriched raised bog pools the quality of dead organic matter and/or the abundance and quality of algae are sufficient to support the whole invertebrate community.

Acknowledgements Nigula Nature Reserve Administration (Estonia) and Staatsbosbeheer (the Netherlands) are acknowledged for giving permission to enter their reserves and to collect samples. Juhan Javoiš, Jan Kuper, Theo Peeters, Maria Judith Sanabria, Michel Smits and Yan Zhuge assisted with the field work and the identification of collected fauna. Jelle Eygensteyn performed all stable isotope measurements. This research project is part of the national research programme 'Survival Plan for Woodland and Nature', funded by the Dutch Ministry of Agriculture, Nature and Food Quality. This is CWE publication nr. 442.

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