LIMNOLOGY and OCEANOGRAPHY

A sprinkling of gold dust: Pine pollen as a carbon source in Baltic Sea coastal food webs

Camilla Liénart [ORCID],[1]* Alyssa R. Cirtwill [ORCID],[1,2] Melanie L. Hedgespeth [ORCID],[3] Clare Bradshaw [ORCID][1]
[1]Department of Ecology, Environment and Plant sciences, Stockholm University, Stockholm, Sweden
[2]Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland
[3]Department of Biology, Lund University, Lund, Scania, Sweden

Abstract

Allochthonous subsidies to marine ecosystems have mainly focused on biogeochemical cycles, but there has also been recent interest in how terrestrial carbon (C) influences marine food webs. In the Baltic Sea, pine (*Pinus sylvestris*) pollen is found in large amounts in shallow bays in early summer. Pollen is a significant C-source in freshwater ecosystems and may also be important in coastal food webs. We examined the consumption of pollen and autochthonous resources by benthic invertebrates in shallow bays of the Baltic Sea. We used stable isotopes to estimate diets and reconstructed consumer-resource networks (food webs) for grazers and particulate organic matter (POM)-feeders to compare how these different guilds used pollen. We found that *P. sylvestris* pollen was consumed in small amounts by a variety of animals and in some cases made up a sizeable proportion of invertebrates' diets. However, invertebrates generally depended less on pollen than other resources. The degree of pollen consumption was related to feeding traits, with generalist invertebrate grazers consuming more pollen (> 10% of diet) than the more specialist POM-feeders (< 5% of diet contributed by pollen). POM-feeders may consume additional microbially-degraded pollen which was not identifiable in our model. We suggest that pollen is a small but substantial allochthonous C-source in shallow bay food webs of the Baltic Sea, with the potential to affect the dynamics of these ecosystems.

The coastal fringe is the interface between marine and terrestrial ecosystems where organisms, nutrients, and detritus from both realms tightly interact (Polis et al. 1997). At this interface, food sources for marine species can either be autochthonous (i.e., locally produced) or allochthonous (imported, e.g., from land). Terrestrial food subsidies to freshwater ecosystems have been relatively well studied, particularly with respect to the role of leaf litter and other plant material in stream and lake food webs (e.g., Marks 2019). Studies of terrestrial inputs to the marine environment have focused more on carbon cycling and biogeochemistry, indicating that inputs

can be several hundred g C m^{-2} yr^{-1} (Gounand et al. 2018), globally equivalent to several hundred Tg C yr^{-1} (Blair and Aller 2012). Fewer studies have focused on these inputs as subsidies to marine and estuarine food webs, but a few case studies have found large amounts of terrestrial carbon consumed as an allochthonous resource in temperate (Dias et al. 2016), Mediterranean (Careddu et al. 2015), and Arctic (Harris et al. 2018) food webs.

The importance of terrestrial organic carbon varies by location. For example, terrestrial organic carbon tends to be a more significant resource close to river outlets (Careddu et al. 2015; Dias et al. 2016) and in the sediment of shallow coastal ecosystems (Watanabe and Kuwae 2015) than in deep waters. Allochthonous subsidies to both freshwater and marine ecosystems are also temporally variable. Inputs tend to occur in short pulses. For example, soil and leaf litter inputs are carried by heavy rain runoffs in autumn or snowmelt in spring (Minshall 1967; Strååt et al. 2016), and pollen deposition occurs seasonally during spring and summer pollination events (Heusser 1988). Despite their spatial and temporal limits, these pulses of allochthonous resource availability can have substantial impacts on the recipient community. Allochthonous inputs can be quite large (e.g., close to 100% of total C inputs in small forest streams,

*Correspondence: camilla.lienart@su.se

Additional Supporting Information may be found in the online version of this article.

Webster and Meyer 1997; and 7–10% of the annual total organic carbon loads in the Baltic Sea, Strååt et al. 2016), offering alternative pathways in food webs and influencing primary consumer populations (Minshall 1967; Careddu et al. 2015; Dias et al. 2016). Although the effect of an allochthonous subsidy on consumer populations is highly context-dependent, studies from a variety of ecosystems suggest that these subsidies can often maintain larger or more stable consumer populations than in situ production (Baxter et al. 2005; Sato et al. 2011, Wallace et al. 2015).

While leaf litter and sediment are often the most obvious allochthonous inputs into aquatic ecosystems, pollen can also be an important source of nutrients and organic matter (Graham et al. 2006). Seasonal pollen pulses can be particularly important in nutrient-poor freshwater ecosystems, where they can increase the biomass of primary producers (Graham et al. 2006), sustain substantial zooplankton populations (Graham et al. 2006; Masclaux et al. 2011), and even influence seasonal variability in zooplankton communities through trophic partitioning from selective grazing on pollen-rich neuston (Masclaux et al. 2013). Pollen is rich in phosphorus (Banks and Nighswander 2000) and polyunsaturated fatty acids and is small enough to be a suitable resource for zooplankton (Masclaux et al. 2011) and benthic organisms (Leduc and Rowden 2018). However, fresh pollen grains are protected by extracellular walls that give them a low food quality (i.e., low digestibility). Like other terrestrial carbon sources, fresh pollen is therefore less bioavailable than autochthonous resources (Dias et al. 2016). As pollen first settles on the water surface and then sinks through the water column, these walls are broken down by fungi or bacteria (Masclaux et al. 2011; Kagami et al. 2017) and become more digestible (i.e., trophic upgrading; Masclaux et al. 2011); thus, pollen's residence time is crucial in determining its use in aquatic food webs.

Despite the importance of pollen as a carbon source in lakes and streams (e.g., 20% of OC incorporated into lake sediments comes from pollen deposition; Doskey and Talbot 2000) and the longstanding use of pollen as a marine palynological marker (Heusser 1988), the role of pollen in coastal marine food webs is not yet known. In large parts of the Baltic Sea, however, pollen has the potential to be a significant food subsidy, particularly in sheltered archipelagos where vegetation grows close to the shore and coastal topography may concentrate wind-driven surface aggregations. Scots pine (*Pinus sylvestris*) is common along these coasts and deposits large amounts of pollen in the early summer. Even several kilometers offshore, pollen may comprise 30–40% of the suspended particulate matter in the Baltic Sea (Pawlik and Ficek 2016), before sinking and becoming part of the sediment. Fresh pollen should, therefore, be available to animals at the surface and high in the water column, as well as in more or less degraded forms to benthic species.

Here, we used stable isotopes to trace the consumption of pollen and autochthonous resources in benthic communities of shallow bays of the Baltic Sea. We used this dietary information to construct consumer-resource networks (food webs) for organisms grazing on macroalgae and aquatic plants (hereafter referred to as grazers) and organisms feeding on suspended or deposited particulate organic matter (POM; hereafter referred to as POM-feeders) in order to compare how these different guilds use pollen. As nutrients in pollen are more available after some amount of microbial decomposition (Masclaux et al. 2011, 2013), we predicted that pollen would form a greater proportion of the diets of POM-feeders which consume degraded pollen than grazers which consume relatively fresh pollen stuck to the surface of algae or epiphytes. We also expected that generalist invertebrate consumers would be more likely to consume and digest pollen than specialists since generalists may have fewer morphological or behavioral barriers preventing them from consuming pollen.

Methods

Study site and sampling

Sampling was conducted close to Stockholm University's Askö Laboratory, located in Stockholm's southern archipelago, in the Baltic Proper, on the 9th and 10th of June 2016, that is, during the peak of the annual Scots pine (*P. sylvestris*) pollen deposition event, which started on the mainland in mid-May according to the national pollen monitoring statistics (Swedish Museum of Natural History 2016). Samples of pollen and benthic invertebrates from two different shallow water habitats (vegetated seabeds and sediment) were taken within a 10 m² area ca. 150 m south of the Askö Laboratory (58°49′18.8″N, 17°38′8.9″E) and plankton samples in the bay immediately west of the field station (58°49′22.5″N, 17°38′2.2″E). The area is nontidal and the coastline comprises a series of small bays (2–10 m across) enclosed by rocky shores which rise 1–2 m above sea level, and pine trees and other vegetation (grasses, lichens) grow close to the water's edge. The seabed comprised a mixture of fine mud and stones of varying size overlying thicker gray clay and was covered with patches of macroalgae and macrophytes interspersed with open sediment. During periods of heavy pollen deposition and onshore winds, thick, yellow accumulations of pollen were seen on the water surface and suspended in the water column in these small bays (Fig. 1).

Pollen was collected from the flowers of five *P. sylvestris* trees growing within 1–2 m of the water line. The flowers were picked into stacked 1 and 0.5 mm sieves in two buckets. The flowers were gently shaken and rubbed on the sieves to release the pollen. The < 0.5 mm fraction was further sieved on a 150 μm sieve and the < 150 μm fraction was preserved under dry and cool conditions until analysis. Floating pollen was skimmed from the water surface where it had accumulated as a thick layer closest to land and sieved immediately through a 150 μm sieve to remove larger debris. The resulting < 150 μm fraction was additionally sieved through a 25-μm sieve. The

Fig. 1. Photo showing the thick accumulation of pine pollen in one of the sampled areas.

25–150 μm fraction was left to stand for 1 h, after which the surface suspension and the settled material ("wet pollen top layer" vs. "wet pollen settled"; *see* Table S1) were pipetted off and frozen separately at $-20°$C to separate pollen fractions at different stages of degradation.

For each habitat (vegetated seabed and sediment), samples of all the dominant shallow-water invertebrates were taken together with as many likely food (i.e., carbon) sources as possible. A full list of samples and subsamples can be found in Table S1, but a description of the sampling methods follows here.

Macrophytes, macroalgae, and their associated mobile invertebrates (*Gammarus* spp., *Idotea* spp., *Jaera albifrons*, *Lymnaea stagnalis*, *Radix balthica*, and *Theodoxus fluviatilis*, chironomid larvae) were collected at 0.3–1 m water depth (maximum 5 m from shore) by a snorkeler. Epiphytic communities were clipped or scraped off both submerged rocks and *Fucus vesiculosus* plants and frozen separately. *Chorda filum* and *F. vesiculosus* were picked and frozen whole. Extra

F. vesiculosus plants were taken to extract associated fauna; all mobile fauna (e.g., isopods, amphipods, gastropods, chironomid larvae) and some sessile species (*Mytilus edulis*, *Amphibalanus improvisus*) were removed and each taxon identified and frozen separately. Sediment and sediment-associated invertebrates (*Cerastoderma glaucum*, *Limecola balthica*) were collected in a sample of 3–4 L from the top 1–2 cm of sediment. The sample was sieved through a 2 mm sieve to extract the infauna. To complete the POM-feeder community, mixed plankton samples were obtained by slowly towing a 15 μm plankton net in surface waters behind a small motorboat.

Subsamples of each plankton sample, suspended pollen sample, and epiphyte sample were preserved in ethanol for subsequent examination under the microscope to determine the species present (*see* Table S1). All invertebrates were frozen at $-20°$C.

Stable isotope analysis

Soft tissues of bivalves, gastropods, and barnacles were analyzed; all other animals and potential food sources were analyzed whole (*see* Table S1). No acid treatment was used. Samples were oven-dried at 60°C, ground to a powder, and packed into tin capsules for stable isotope analysis. Where necessary, individual animals were pooled to achieve sufficient sample weight (*see* Table S1). Samples were analyzed for ^{13}C and ^{15}N at the UC Davis Stable Isotope Facility (University of California, Davis, California) with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.). Stable isotope ratios were expressed in permil (‰) following the classical δ notation:

$$\delta X = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000$$

where X is ^{13}C or ^{15}N and R the isotopic ratios ^{13}C/^{12}C or ^{15}N/^{14}N, respectively, and the references are Vienna Pee Dee Belemnite for δ^{13}C and atmospheric N_2 for δ^{15}N. Analytical uncertainties were 0.2 for ^{13}C and 0.3 for ^{15}N.

Food webs and selection of resources

Two food webs were defined based on both the habitat (vegetated or sediment) and feeding mode of the different species. The first food web (grazer web) included taxa associated with vegetation and mainly relying on algae, plants, or their epiphytes and biofilm for food: *Gammarus* spp. ($n = 8$), *Idotea* spp. ($n = 5$), *J. albifrons* ($n = 5$), *R. balthica* ($n = 9$), *T. fluviatilis* ($n = 10$), *L. stagnalis* ($n = 1$), and chironomid larvae (Chironomidae; $n = 8$). The second food web (POM-feeder web) included invertebrates sampled in sediment and sessile species sampled in vegetation that rely on planktonic or sedimentary POM as food sources: *C. glaucum* ($n = 7$), *L. balthica* ($n = 5$), *M. edulis* ($n = 5$), and *A. improvisus* ($n = 5$). Note that n refers to the number of samples, not individuals; *see*

Table S1 for details. Variable sample size reflects different field abundances of these taxa.

The selection of possible food sources to be included in the models was based on (1) prior knowledge of invertebrate diets and (2) on the positioning of invertebrate as "consumers" and their potential resources in the isospace plot source-polygon (corrected for trophic enrichment factor) following literature recommendations (Phillips et al. 2014; Stock et al. 2018). For each food web, redundant resources (i.e., those with similar isotope signal, functional similarity, or both) were averaged into more generic resource types: plankton, brown algae (*F. vesiculosus* + *C. filum*), and epiphytes (from *Fucus* and stones). The initial source-polygon did not fully frame the invertebrate consumer data in the isospace plot of the grazer web. Based on ecosystem knowledge, we identified an additional resource likely available to the invertebrates in the grazer web, the aquatic plants (*Stuckenia pectinata*, a submerged angiosperm, and *Chara* spp. an aquatic charophyte), whose isotope signals allowed us to frame the invertebrate consumer values. Similarly, sedimentary POM is an important resource for suspension-feeders and was missing in the POM-feeder web. As these two food sources were not collected during initial sampling, we used isotope values for these food sources from a study by Hansen et al. (2012) which sampled the same area. In the end, four food sources (final values used for modeling; Table 1) were used to run each of the two models as recommended by the MixSIAR package guidelines and literature (i.e., ideally the number of tracers +1, although more sources are also accepted; Fry 2013). Pollen and brown algae were considered as potential resources for both webs, sedimentary POM, and plankton were selected as food sources for the POM-feeder web and aquatic plants and epiphytes were used in the grazer web model. Almost all invertebrate values were within the source-polygon for both food webs.

Stable isotope mixing models

To estimate the proportion of resources contributing to invertebrates' diets, stable isotope values of carbon and nitrogen δ^{13}C and δ^{15}N were used in a Bayesian mixing models that account for variability in the source and mixture tracer data when estimating source contributions (*MixSIAR* R package, version 3.1.10; Stock et al. 2018; R Core Team 2018). In the absence of a clear scientific consensus on trophic enrichment factor values to be used (*see* Supplementary Information, Supplementary Methods section), the trophic enrichment factor for δ^{13}C and δ^{15}N was defined following a classical and rather conservative approach: for all resources and organisms of both webs (since all invertebrates sampled herein were herbivorous primary consumers, poikilotherms, and ammonotelic organisms), the same trophic enrichment factor was used (δ^{13}C = 0.4 ± 0.2‰, δ^{15}N = 2.4 ± 0.3‰; calculated based on average of McCutchan et al. 2003; Vanderklift and Ponsard 2003). Another approach estimating the trophic enrichment factor from an equation based on a study from Caut et al. (2009) was also explored and is described in the Supplementary Information (results Table S3b).

Models were run for the two food webs separately (POM-feeder web: 4 taxa; grazer web: 7 taxa) for each individual invertebrate stable isotope data. We used taxon as a fixed effect, a "generalist" prior ($p \sim$ Dirichlet (α) with p the estimated vector of proportions and α a mixture of x components or sources, 4 in our case, $\alpha = c(1,1,1,1)$, referred to as generalist prior because every possible set of proportions has equal probability), as we had no prior knowledge about the animals' diet. We included both residual and process error terms, and set the Markov chain Monte Carlo chains (MCMC) as "normal run" as suggested by Stock et al. (2018), in the *MixSIAR* GUI user manual and *MixSIAR* package guide. Following Stock et al. (2018) recommendations, model outputs were evaluated with Gelman-Rubin and Geweke convergence diagnostics and, according to both, the MCMC chains in all of our models converged. Normalized surface area of the food source polygon and posterior distribution plots for each resource were checked (i.e., to avoid bimodal or widespread distribution) as additional criteria. Results represent the probability distribution of feasible dietary proportions produced by the models and are expressed as the percentage of resource contribution calculated from the median of the distribution (50%). The absolute

Table 1. Final stable isotope values (i.e., averages [mean ± SD] or literature values) for all potential food sources used in mixing model calculations for the two food webs (n = number of samples, some comprising pooled individuals [macrophytes]; *see* Table S1 for sampling details and raw isotope data).

Food source (*n*)	δ^{13}C (‰)	δ^{15}N (‰)	Food web	Description
Pollen (9)	−28.2±0.6	−0.5±0.7	Both	Wet pollen (surface top layer and settled)
Sedimentary POM (6)	−19.4±1.2	1.9±0.8	POM-feeder	Sedimentary POM (from Hansen et al. 2012)
Plankton (10)	−24.4±0.3	4.1±0.5	POM-feeder	35–200 μm and >200 μm mixed plankton samples
Brown algae (20)	−12.3±1.4	3.9±0.8	Both	Marine brown algae *F. vesiculosus* and *C. filum*
Aquatic plants (12)	−11.5±1.5	0.01±3.1	Grazer	Freshwater angiosperm Charophytes (*Chara* sp.) and *Stuckenia pectinata* (from Hansen et al. 2012)
Epiphytes (15)	−17.0±2.4	3.2±1.3	Grazer	Epiphytes collected from *Fucus* and stones

uncertainty associated with the mixing-model outputs was generally close to 10%.

Network analysis

After identifying invertebrates' diets using stable isotopes analyses, we used this diet information to construct weighted food web adjacency matrices. These webs link invertebrates and the resources they consume, with weights reflecting the proportion of each invertebrate's diet contributed by each resource. These networks provide a description of the POM-feeding and grazing communities as integrated wholes and allow us to compare pollen to other resources, as well as identify common characteristics of invertebrates which do and do not consume substantial amounts of pollen.

We were first interested in whether pollen was used differently from other resources and whether usage of pollen differed between POM-feeders and grazers. We therefore measured the extent to which invertebrates are specialized on particular resources (consumer specificity). Specificity is defined as the coefficient of variation in the distribution of link weights (here, proportion of an invertebrate's diet contributed by a resource), following Poisot et al. (2012).

$$S_i = \frac{\sqrt{\sum_i (P_i - \mu)^2}}{\mu n_C \sqrt{\frac{n_C - 1}{n_C}}} \tag{1}$$

where S_i is the specificity of resource i, P_i is the vector of links involving resource i, μ is the mean link weight across the entire web, and n_c (R in Poisot et al. 2012) is the number of invertebrate taxa. This is a normalization of the "species specificity index" in Julliard et al. (2006) such that a value of 0 represents a resource which contributes the same proportion of all invertebrates' diets and 1 represents a resource eaten by only one taxa. We calculated specificity using the function "specieslevel" of the *bipartite* R package (Dormann 2011; R Core Team, 2018).

We tested how consumer specificity varied with the proportion of pollen in the diet (i.e., whether any invertebrate specialized on pollen, and whether generalists or specialists consumed more pollen) and how this differed between the POM-feeder and grazer webs. We tested this statistically by fitting a beta regression of proportion of pollen in the diet against consumer specificity, web type (grazers or POM-feeders) and their interaction. We fitted the regression using the R (R Core Team 2018) function "betareg" from the package *betareg* (Grün et al., 2012).

Next, we considered network properties of the resources. We calculated the extent to which the invertebrate community *as a whole* depended on each resource (resource strength, defined in Bascompte et al. 2006 as the sum of the weights of all links to a resource) and whether or not all invertebrates tended to use a resource equally (resource specificity, defined as above for invertebrate consumers). We expected a key resource to have a high strength (many invertebrates

depending strongly on the resource) and low specificity (many invertebrates using the resource at similar proportions).

Within a network, resource strengths sum to the number of consumers (here, invertebrates). In order to compare resource strengths across our differently-sized networks, we normalized resource strengths by the number of invertebrates in the focal web:

$$M_r = \frac{\sum (p_{rc})}{n_c} \tag{2}$$

where M_r is the normalized strength of resource r, p_{rc} is the proportion of resource r in the diet of invertebrate consumer c, and n_c is the number of consumers.

This normalized strength was thus equivalent to the average proportion of invertebrates' diets contributed by a resource. A strength of 0 meant a resource was not eaten by any invertebrate, while a strength of 1 indicated a resource which was the only food source for all invertebrates. Specificity as defined above was automatically normalized between 0 (used by all invertebrates equally) and 1 (used by a single invertebrate) and was therefore comparable across networks without modification. We calculated strengths and specificities using the R (R Core Team) function "grouplevel" from the package *bipartite* (Dormann et al. 2008, Dormann 2011).

In a food web based on stable isotope data, it is difficult to definitely eliminate potential resources from the diets of invertebrates. Weak links may be artifacts of the mixing model rather than true components of invertebrates' diets. To control for the possibility that such artifacts might influence our conclusions, we removed all links < 10% and re-ran the analysis. All results were similar to those obtained using all links, suggesting that our results are robust to the inclusion of some false weak links (*see* Supplementary Information, Tables S5, S6).

Results

δ^{13}C and δ^{15}N of resources and invertebrate consumers

The stable isotope signal of potential food sources was well discriminated for both food webs (Fig. 2; Table 1). Pollen had the lowest δ^{13}C whereas brown algae and aquatic plants had the highest values. Plankton, which was a mix of phyto- and zooplankton and some suspended pollen, had a δ^{13}C closer to the pollen signal. Sedimentary POM (i.e., also a mixed resource) had values between those of macrophytes and plankton. Pollen δ^{15}N was the lowest of all resources whereas plankton had the highest values. Epiphytes and brown algae had higher δ^{15}N values than sedimentary POM and aquatic plants.

On average, the taxa from the grazer web had higher δ^{13}C with the highest values for *T. fluviatilis* and *Idotea* spp. ($-14.4 \pm 0.9‰$ and $-14.8 \pm 0.4‰$, respectively) whereas taxa from the POM-feeder web had lower δ^{13}C with the lowest values for *M. edulis* and *C. glaucum* ($-21.3 \pm 0.8‰$ and $-20.6 \pm 2.1‰$, respectively) (Fig. 2; Table S1). The lowest

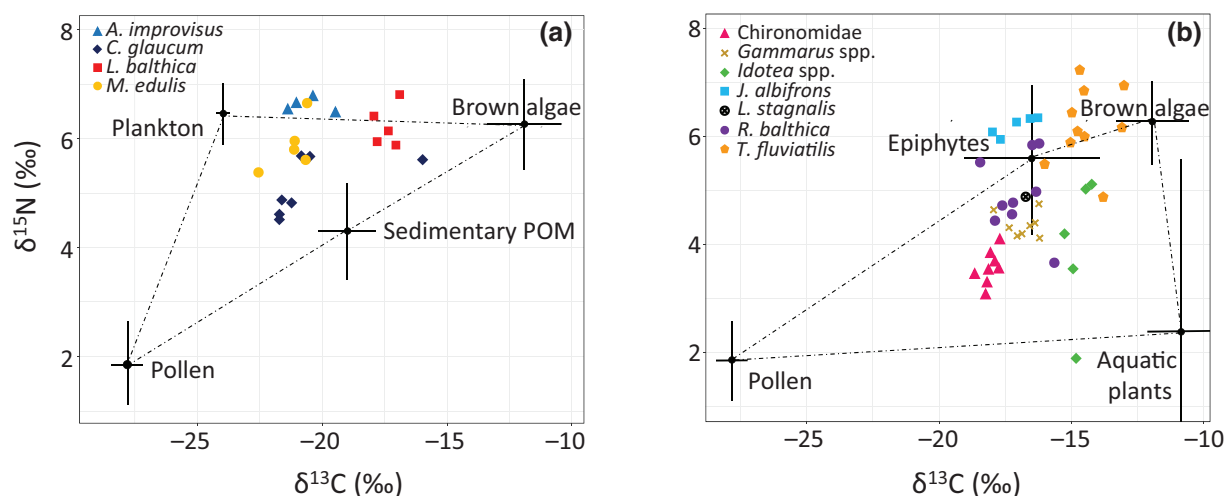**Fig. 2.** Isospace plot (δ^{13}C and δ^{15}N) of food sources (black circles; average ± standard deviation) and invertebrates (individual values) for (**a**) POM-feeder and (**b**) grazer webs. Food sources isotope values are corrected with trophic enrichment factor. Raw data and biplot are given in supplemental material. Note that MixSIAR model uses the source + discrimination values to fit the mixture data (the isospace plot adds the discrimination means and SDs to the raw source values).
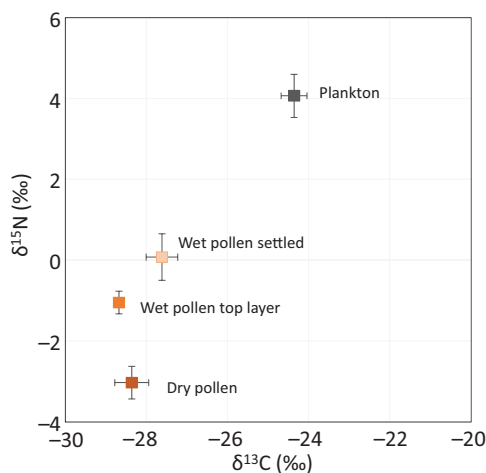

Fig. 3. Biplot of different fractions of pollen and plankton (average ± standard deviation). "Dry pollen" is straight from the tree. "Wet pollen top layer" and "wet pollen settled" are the floating and settled fractions of the suspended pollen, respectively, and the average of the two "Wet pollen" fractions was used as a resource in the mixing models (Table 1). The resource "Plankton" is used in the mixing models. For more details, *see* Table S1.

δ^{15}N were observed in the grazer web for Chironomidae and *Gammarus* spp. (3.6 ± 0.3‰ and 4.4 ± 0.2‰ respectively) whereas higher δ^{15}N were observed in both webs, with the highest values for *A. improvisus* (6.6 ± 0.1‰) in the POM-feeder web and *T. fluviatilis* (6.2 ± 0.7‰) in the grazer web (Fig. 2; Table S1).

In the water column, the pollen δ^{15}N signal differed while settling (Fig. 3). Dry pollen had negative values ($-3.0 ± 0.4$‰) that became less negative as the pollen settled out of the water column ("wet pollen settled" $0.1 ± 0.6$‰ in Fig. 3). The plankton signal followed the opposite trend, with positive δ^{15}N decreasing as the plankton settled out, converging with the wet settled pollen signal. Note also that the settled pollen and plankton samples were less pure than "dry pollen" and non-settled plankton (*see* Table S1).

Invertebrates' diets and specificity

POM-feeders generally relied on plankton as a primary food source and brown algae (i.e., shredded particles) as a secondary food source, while sedimentary POM and pollen made more minor contributions (except for *C. glaucum*, which consumed mainly sedimentary POM; Fig. 4). Most grazers obtained most of their diet from epiphytes and/or brown algae (Fig. 4), with the exception of *Idotea* spp. that mainly consumed aquatic plants, and Chironomidae that mainly consumed pollen.

Pollen made the largest contribution to the diets of chironomids larvae and was also an important food source for *Gammarus* spp. and *L. stagnalis* (33.5 ± 2.6%, 27.1 ± 4.1%, and 22.8 ± 7.5% of their diets from pollen, respectively, Table S3). POM-feeders used very little pollen (< 5%; Fig. 4; Table S3).

Across both webs, species with lower specificity consumed significantly more pollen (specificity = -3.68, $p < 0.001$; Fig. 5). The main effect of web type (POM-feeder or grazer) and interaction between web type and specificity were not significant (web type = -3.49, $p = 0.456$; web type: specificity = 4.16, $p = 0.653$). Note, however, that our
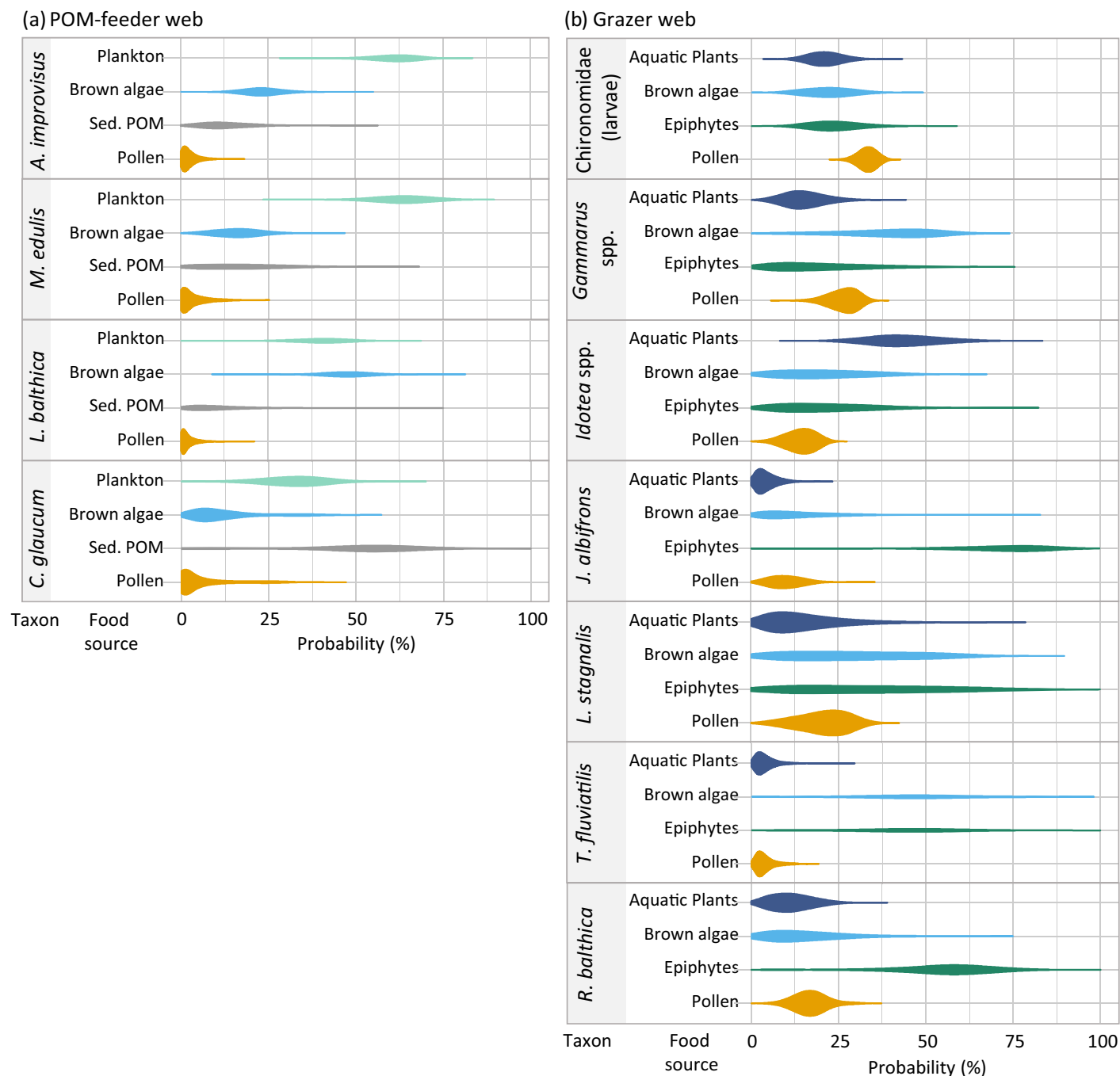
Fig. 4. Mixing model posterior distributions (%) of invertebrates' diet composition (the widest part of each violin plot represents the median probability for that specific resource) for (**a**) POM-feeder web and (**b**) Grazer web. Median and standard deviations are presented in Table S3. Sed. POM is sedimentary particulate organic matter.

sample size for this regression was quite small ($n = 7$ for the grazer web and $n = 4$ for the POM-feeder web), and thus the statistical power to detect a relationship is low. In addition, the POM-feeding invertebrates had very similar specificities and levels of pollen consumption. Because of these facts, we cannot conclude whether or not the POM-feeders

show the same relationship between specificity and pollen consumption as the invertebrates in the grazer web.

Network properties of pollen and other resources

    In the POM-feeder web, pollen had by far the lowest strength but similar specificity to plankton (Fig. 6; Table S4)
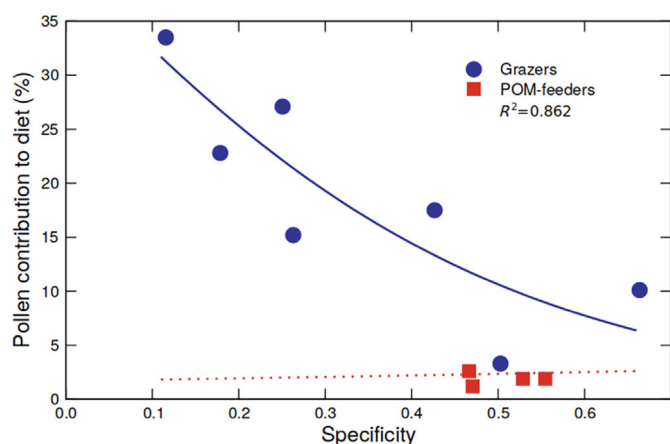
Fig. 5. Proportion of pollen in the diet of invertebrate consumers decreased significantly as the specificity of each taxon increased in the grazer-web (blue circles, solid blue line; $p = 0.007$) but not the POM-feeder web (red squares, dotted red line; *see* Table S3). Specificity describes the extent to which an invertebrate diet is dominated by a single resource: 0 is extreme generalist and 1 complete specialist. Lines indicate predicted amount of pollen consumed against specificity for each web type (POM-feeder or grazer) based on a beta regression of amount of pollen consumed against specificity, web type (POM-feeder or grazer), and their interaction. R^2 refers to the same beta regression. With web type = grazer as the baseline, the main effect of web type and the interaction between web type and specificity were not significant. Phi = 59.3, $p = 0.022$, log-likelihood = 22.5 on 5 degrees of freedom. Pseudo R^2: 0.862.

suggesting that pollen was consumed in similarly small amounts by all invertebrates. In the grazer web, pollen had second-lowest strength and second-highest specificity. Since strength reflects the average proportion of a food source in the diet of all invertebrate consumers while specificity reflects the extent to which pollen consumption is dominated by specific invertebrates, this finding suggests that pollen was consumed in relatively small amounts by most invertebrates while allochthonous primary producers were used less selectively and consumed in larger amounts.

Discussion

We found that *P. sylvestris* pollen was consumed in small amounts by many animals in shallow bays of the Baltic Sea, and in some cases (e.g., chironomid larvae) made up a sizeable proportion of the invertebrates' diet (Fig. 7). In general, the more generalist an invertebrate is (or a consumer from a network perspective), the more pollen it consumed. Contrary to our expectations, grazers tended to consume more pollen than POM-feeders. The POM-feeders we considered obtained less than 5% of their diet from pollen. For these invertebrates, apparent pollen consumption may be an artifact of including pollen in the mixing models rather than a true feeding link. The grazers, on the other hand, obtained much larger proportions of their diets from pollen (up to 33% for Chironomidae).

Such strong links suggest that pollen is a true resource for Baltic Sea invertebrates at this time of year when it is plentiful, and should be considered as part of the food web.

Invertebrate feeding traits determine degree of pollen consumption

In the grazer web, less-specialized invertebrates tended to consume more pollen (Fig. 5; Table S4). Invertebrates' feeding traits can help explain this trend, as well as the higher consumption of pollen in the grazer web compared to the POM-feeder web. Intact pine pollen is large ($\sim 50\,\mu$m; own data; Masclaux et al. 2013; Pawlik and Ficek 2016) compared to the range of particle sizes consumed by most of the POM-feeders we considered (*M. edulis*: 2–20 μm; *L. balthica*: 10–50 μm; *A. improvisus*: wide range of particle size overlapping with *Mytilus*; Ward and Shumway 2004 and references therein). The POM-feeder which ingests the largest particles, *C. glaucum* (60–500 μm; Ward and Shumway 2004 and references therein) ingests particles larger than a single pollen grain. Intact pollen is therefore probably not a suitably-sized resource for the POM-feeders we considered.

The grazers in our food web target large food sources (e.g., brown algae), their epiphytes and surface biofilms, or both. Most have low specificities and are likely to accidentally consume pollen grains on the surface of their intended food. The amphipods *Gammarus* spp. and the gastropod *L. stagnalis*, which consumed substantial amounts of pollen, are generalist omnivores that mainly consume macroalgae as well as filamentous algae (Orav-Kotta et al. 2009; Zhang et al. 2018). As omnivores, they are likely to be able to digest a wide range of foods, including pollen grains trapped in the epiphytic filamentous algae (Table S1). The exceptions to this trend are the snail *T. fluviatilis* and the tiny isopod *J. albifrons*, which mainly scour and abrade young macrophytes, epiphytes, and algal or bacterial films from rocks or macrophytes (Jones 1972; Skoog 1978; Korpinen et al. 2008). Our data suggest that *J. albifrons* is more specialized (on epiphytes) than any other grazer, while *T. fluviatilis* consumes both epiphytes and brown algae. However, both seem to actively avoid consuming pollen or cannot digest it, either of which would result in the SI ratios we observe (ingestion does not necessarily imply digestion and assimilation, e.g., Pitt et al. 2009). The two constraints of being able to ingest and digest pollen-sized particles and thus to take advantage of multiple resources (including transient resources such as pollen) likely explain much of the variation in pollen consumption between our invertebrates and may also be important in understanding how other allochthonous resources are integrated into Baltic Sea food webs.

In our study, chironomid larvae consumed the most pollen. There are an estimated 230 species of Chironomidae in the Baltic (Brodin et al. 2013) and, as chironomid taxonomy is notoriously difficult, the larvae in our study were not identified below family level. The Chironomidae in our study were found in the algae and plant samples. Their exact feeding
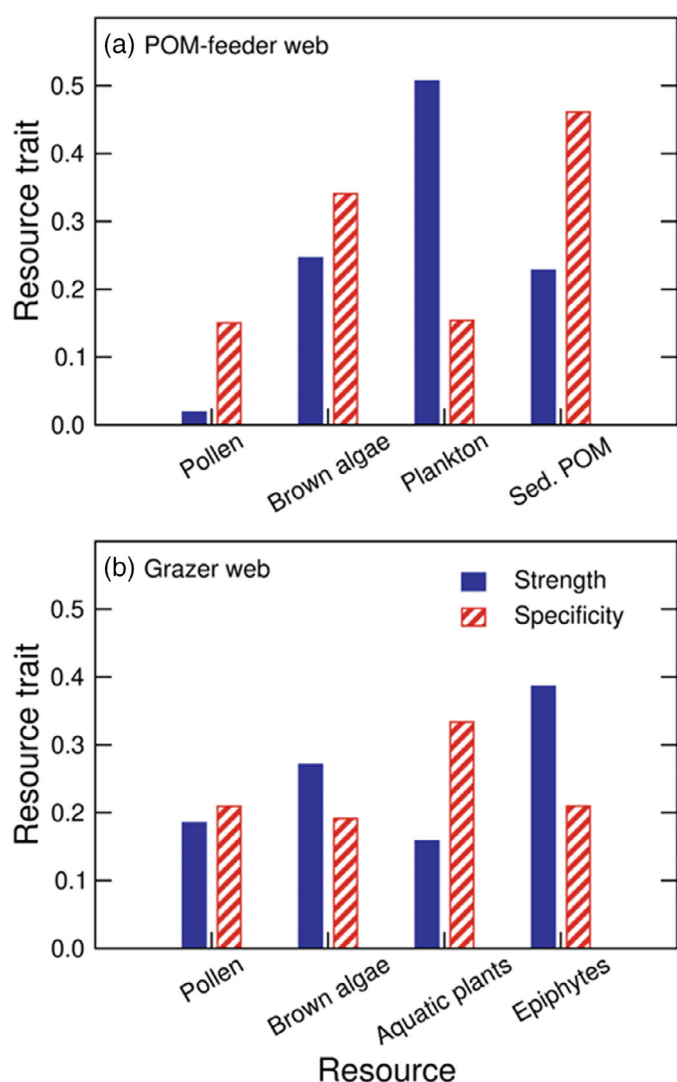
Fig. 6. Species strength and specificity for resources in near-shore Baltic food webs. Strength (solid blue bars) is the sum of invertebrate consumer dependencies on a resource, while specificity (striped red bars) describes the extent to which the resource's consumption is dominated by a single invertebrate (higher specificity means more consumption by a single invertebrate consumer). For ease of comparison between webs, strength values have been normalized by dividing by the number of invertebrates (seven in the [**b**] grazer web and four in the [**a**] POM-feeder web). This normalized strength is the average proportion each resource contributes to the diets of all invertebrates. Sed. POM is sedimentary particulate organic matter.

habits are unknown, however, and chironomid larvae show a wide range of feeding modes (e.g., predators, detritivores, filter-feeders, and grazers) as well as having a great flexibility in diet and showing opportunistic feeding behavior (Berg 1995; Reuss et al. 2013). Consistent with our results, Kornijów et al. (2019) found that ca. 70–90% of chironomid larvae sampled in May–July on the Polish Baltic coast contained pine pollen in their guts; pollen was one of the most frequently occurring food items found regardless of whether

the species was a filter-feeder or deposit-feeder. In addition, many chironomid larvae have a short life time (2–3 weeks; Berg 1995), and thus a fast tissue turnover, and are likely to display a particularly strong signal when using a transient and pulsed resource like pollen. Pollen consumption by chironomid larvae in other habitats (e.g., freshwater) may deserve further study.

Pollen: A transient but substantial C-source

Pollen is only nutritionally available for a few weeks per year (Rösel et al. 2012), although the cell walls can persist for millennia (Heusser 1988). It can be highly spatially variable, especially on the water surface, as winds can quickly redistribute pollen aggregates (Pawlik and Ficek 2016). A pollen-specialist consumer would therefore need to complete its life cycle during the brief period of pollen availability, while generalists can take advantage of the pollen windfall and use other food sources after pollen has been buried or fully degraded.

The total biomass of pollen available to aquatic food webs is low (up to 10% of the organic carbon flux to lakes; Doskey and Talbot 2000) compared to that of autochthonous resources like plankton and macroalgae. It is not surprising that a less abundant resource is consumed in smaller quantities than common autochthonous resources and therefore has lower strength within the food web. However, pollen is rich in phosphorus and polyunsaturated fatty acids, although its extracellular wall makes it a poorly digestible resource (Banks and Nighswander 2000; Masclaux et al. 2011) that needs microbial degradation to be nutritious (Masclaux et al. 2011; Kagami et al. 2017). After some degradation, pollen may become a high-quality resource for the species that do consume it. The quality of an allochthonous subsidy can have greater effects on the recipient community than its quantity (Bartels et al. 2012), suggesting that pollen may be more significant than its low biomass suggests, particularly at those times of year when deposition events occur.

The amount of pollen consumed by POM-feeders in our study may also be underestimated. As pollen degrades and is mixed with plankton in the water column, its isotopic ratio becomes increasingly similar to that of fresh plankton (Fig. 3). In our model, both pollen and plankton were considered as mixtures of various stages of degradation and different proportions of the "pure" sources (fresh pollen and isolated phyto- or zooplankton). The observed increase in $\delta^{15}N$ signal of settling pollen can be the result of the mixing of these different sources or due to the use of marine dissolved inorganic nitrogen by colonizing bacteria and fungi on the pollen particle. This mixing could result in invertebrates, especially POM-feeders that ingest a large amount of heavily microbially-degraded or mixed pollen (higher $\delta^{15}N$ signal), being assigned a larger proportion of plankton consumption than they truly eat and may explain why POM-feeders have less pollen contribution to their diet than grazers. In addition, we only
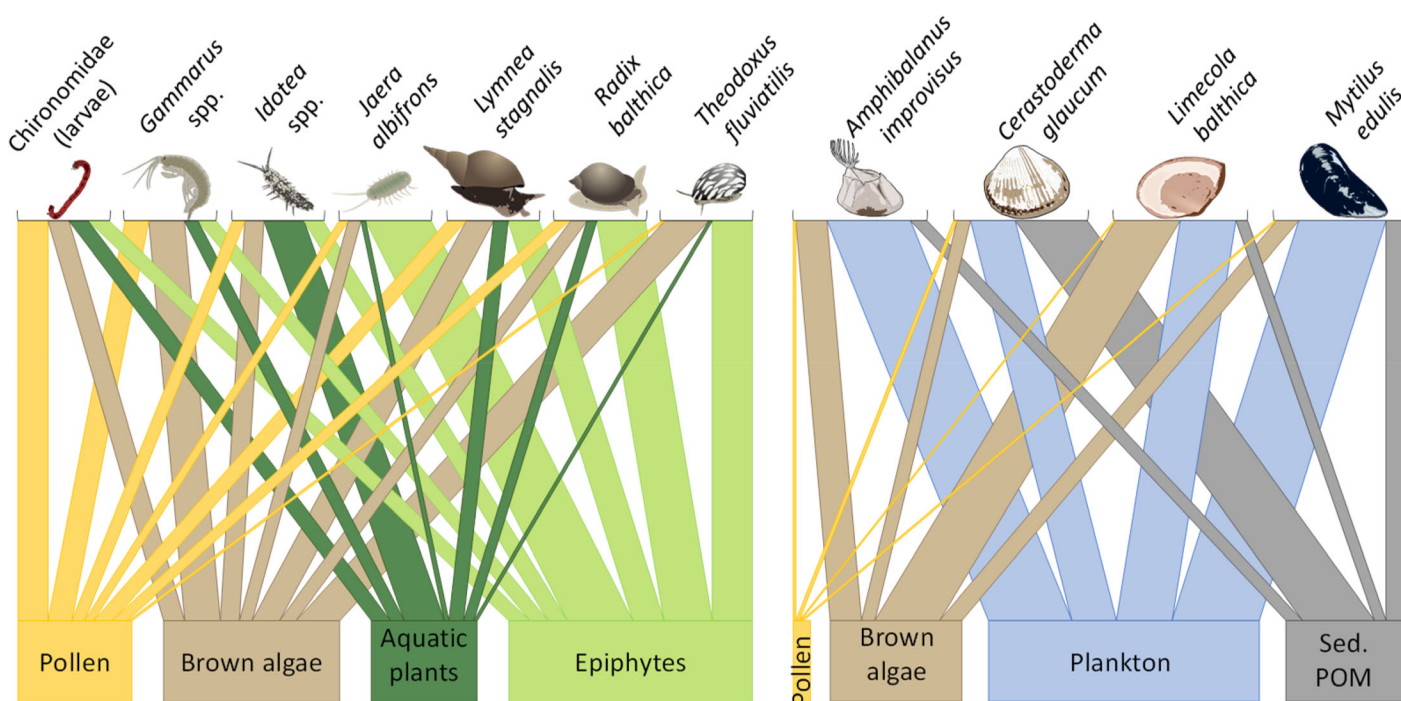
Fig. 7. Summary of the weighted feeding links for the grazer and POM-feeder food webs of this study. The thickness of the link represents the relative contribution of each food source (%, *see* values Table S3) to the diet of invertebrate consumers. Width of boxes for food sources indicate the overall contribution of each source to the food web (assuming that all consumers take in similar amounts of biomass). Sed. POM is sedimentary particulate organic matter.

included pine pollen in our analyses. However, other wind-pollinated species such as birch also likely deposit large amounts of pollen into shallow bays, which may be consumed in similar ways to pine pollen and could also increase the contribution of pollen to invertebrates' diets.

Role of pollen in shallow bay communities

The overall influence of pollen on shallow bay food webs is difficult to predict without more detailed knowledge of the population dynamics of invertebrates, the seasonal dynamics of pollen inputs compared to other resources, etc. Nevertheless, we can speculate based on pollen's place in the food webs we observed. Simulations suggest that allochthonous inputs can be stabilizing if they are small relative to in situ production and if animals do not strongly prefer the allochthonous resource (Huxel and McCann 1998)—both criteria apply to pollen. When allochthonous resources are available, generalists may consume these resources rather than autochthonous food sources, reducing competition with specialists and allowing for higher populations of invertebrates (Spiller et al. 2010; Sato et al. 2011). In our study, pollen is mainly consumed by generalists and it is plausible that these invertebrates switch freely between pollen and other resources, depending upon what is available, and could allow pollen to reduce competition between consumers and maintain

higher populations, as seen in other ecosystems (Huxel and McCann 1998; Spiller et al. 2010).

The future impact of pollen on Baltic Sea food webs is likely to be shaped by the decoupling of pollen and autochthonous resources. Currently, pine pollen coincides with the peak availability of some filamentous algae (i.e., early June in our area; Kautsky et al. 2017) but after the main phytoplankton spring bloom and before the main summer bloom, both of which also provide a pulse of POM to the seabed (Griffiths et al. 2017). However, pollen inputs depend on wind and terrestrial runoff (Pawlik and Ficek 2016), as well as terrestrial conditions affecting tree health, rather than coastal nutrient status which drives allochthonous primary production. This variety of influences on pollen deposition means that pollen availability is both highly spatially and temporally variable and is likely to respond differently to climate change and other ongoing anthropogenic pressures than autochthonous resources. Depending upon whether the availabilities of pollen and autochthonous resources change at similar rates, the effect of pollen on Baltic Sea invertebrates' populations may vary over time.

Conclusions

Our results show that *P. silvestris* pollen is a carbon source that substantially contributes to benthic food webs, providing

ca. 20% of the diet for generalist grazers, during this short time window in shallow bays in the Baltic Sea. Terrestrial organic carbon can complement locally produced resources in terms of quality and timing. If pollen is available during times when other resources are scarce, it could provide a buffer for changing availability of autochthonous resources. However, whether and how pollen inputs to marine ecosystems are likely to change over time has not yet been studied to our knowledge. Understanding the dynamics of interface habitats like shallow bays requires researchers to consider allochthonous resources together with in situ production, and our results suggest that pollen is an allochthonous resource worthy of further study.

References

Banks, H. H., and J. E. Nighswander. 2000. Relative contribution of hemlock pollen to the phosphorus loading of the clear lake ecosystem near Minden, Ontario, p. 168–174. *In* K. A. McManus, K. S. Shields, and D. R. Souto [eds.], Proceedings: Symposium on sustainable management of hemlock ecosystems in eastern North America. General Technical Report NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. https://www.nrs.fs.fed.us/pubs/4698

Bartels, P., J. Cucherousset, K. Steger, P. Eklov, L. J. Tranvik, and H. Hillebrand. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology **93**: 1173–1182. doi:10.1890/11-1210.1

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymetric coevolutionary networks facilitate biodiversity maintenance. Science **312**: 431–434. doi:10.1126/science.1123412

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. **50**: 201–220. doi:10.1111/j.1365-2427.2004.01328.x

Berg, M. B. 1995. Chapter 7: Larval food and feeding behaviour, p. 136–168. *In* P. D. Armitage, L. C. Pinder, and P. Cranston [eds.], The Chironomodae: Biology and ecology of non-biting midges. Springer. doi:10.1007/978-94-011-0715-0_7

Blair, N. E., and R. C. Aller. 2012. The fate of terrestrial organic carbon in the marine environment. Ann. Rev. Mar. Sci. **4**: 401–423. doi:10.1146/annurev-marine-120709-142717

Brodin, Y., G. Ejdung, J. Strandberg, and T. Lyrholm. 2013. Improving environmental and biodiversity monitoring in the Baltic Sea using DNA barcoding of Chironomidae (Diptera). Mol. Ecol. **13**: 996–1004. doi:10.1111/1755-0998.12053

Careddu, G., M. L. Costantini, E. Calizza, P. Carlino, F. Bentivoglio, L. Orlandi, and L. Rossi. 2015. Effects of terrestrial input on macrobenthic food webs of coastal sea are detected by stable isotope analysis in Gaeta Gulf. Estuar. Coast. Shelf Sci. **154**: 158–168. doi:10.1016/j.ecss.2015.01.013

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): The effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. **46**: 443–453. doi:10.1111/j.1365-2664.2009.01620.x

Dias, E., P. Morais, A. M. Cotter, C. Antunes, and J. C. Hoffman. 2016. Estuarine consumers utilize marine, estuarine and terrestrial organic matter and provide connectivity among these food webs. Mar. Ecol. Prog. Ser. **554**: 21–34. doi:10.3354/meps11794

Dormann, C. F. 2011. How to be a specialist? Quantifying specialisation in pollination networks. Netw. Biol. **1**: 1–20.

Dormann, C. F., Gruber, B., and J. Fründ. 2008. Introducing the bipartite Package: Analysing Ecological Networks. R News. Vol. ISSN 1609-3631.

Doskey, P. V., and R. W. Talbot. 2000. Sediment chronologies of atmospheric deposition in a precipitation-dominated seepage lake. Limnol. Oceanogr. **45**: 895–904. doi:10.4319/lo.2000.45.4.0895

Fry, B. 2013. Minmax solutions for underdetermined isotope mixing problems: Reply to Semmens and others. (2013). Mar. Ecol. Prog. Ser. **490**: 291–294. doi:10.3354/meps10536

Gounand, I., C. J. Little, E. Harvey, and F. Altermatt. 2018. Cross-ecosystem carbon flows connecting ecosystems worldwide. Nat. Commun. **9**: 4825. doi:10.1038/s41467-018-07238-2

Graham, M. D., R. D. Vinebrooke, and M. Turner. 2006. Coupling of boreal forests and lakes: Effects of conifer pollen on littoral communities. Limnol. Oceanogr. **51**: 1524–1529. doi:10.4319/lo.2006.51.3.1524

Griffiths, J. R., M. Kadin, F. J. A. Nascimento, and others. 2017. The importance of benthic – pelagic coupling for marine ecosystem functioning in a changing world. Glob. Chang. Biol. **23**: 2179–2196. doi:10.1111/gcb.13642

Grün, B., I. Kosmidis, and A. Zeileis. 2012. Extended beta regression in R: Shaken, stirred, mixed, and partitioned. J. Stat. Soft. **48**: 1–25. doi:10.18637/jss.v048.i11

Hansen, J. P., S. A. Wikström, and L. Kautsky. 2012. Taxon composition and food-web structure in a morphometric gradient of Baltic Sea land-uplift bays. Boreal Environ. Res. **17**: 1–20.

Harris, C. M., N. D. McTigue, J. W. McClelland, and K. H. Dunton. 2018. Do high Arctic coastal food webs rely on a terrestrial carbon subsidy? Food Webs **15**: e00081. doi:10.1016/j.fooweb.2018.e00081

Heusser, L. E. 1988. Pollen distribution in marine sediments on the continental margin off northern California. Mar. Geol. **80**: 131–147. doi:10.1016/0025-3227(88)90076-X

Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. Am. Nat. **152**: 460–469. doi:10.1086/286182

Jones, M. B. 1972. The mouthparts of the members of the *Jaera albifrons* group of species (Crustacea: Isopoda). Mar. Biol. **14**: 264–270. doi:10.1007/BF00348290

Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. **9**: 1237–1244. doi:10.1111/j.1461-0248.2006.00977.x

Kagami, M., Y. Motoki, H. Masclaux, and A. Bec. 2017. Carbon and nutrients of indigestible pollen are transferred to zooplankton by chytrid fungi. Freshw. Biol. **62**: 954–964. doi:10.1111/fwb.12916

Kautsky, H., G. Martin, and P. Snoeijs-Leijonmalm. 2017. Chapter 11: The phytobenthic zone, p. 387–455. *In* P. Snoeijs-Leijonmalm, H. Schubert, and T. Radziejewska [eds.], Biological oceanography of the Baltic Sea. Springer. doi:10.1007/978-94-007-0668-2_11

Kornijów, R., M. Markiyanova, and E. Lange. 2019. Feeding by two closely related species of *Chironomus* (Diptera: Chironomidae) in south Baltic lagoons, with implications for competitive interactions and resource partitioning. Aquat. Ecol. **53**: 315–324. doi:10.1007/s10452-019-09691-7

Korpinen, S., V. Jormalainen, and J. Ikonen. 2008. Selective consumption and facilitation by mesograzers in adult and colonizing macroalgal assemblages. Mar. Biol. **154**: 787–794. doi:10.1007/s00227-008-0971-6

Leduc, D., and A. A. Rowden. 2018. Not to be sneezed at: Does pollen from forests of exotic pine affect deep oceanic trench ecosystems? Ecosystems **21**: 237–247. doi:10.1007/s10021-017-0146-8

Marks, J. C. 2019. Revisiting the fates of dead leaves that fall into streams. Annu. Rev. Ecol. Evol. Syst. **50**: 547–568. doi:10.1146/annurev-ecolsys-110218-024755

Masclaux, H., A. Bec, M. Kagami, M. E. Perga, T. Sime-Ngando, C. Desvilettes, and G. Bourdier. 2011. Food quality of anemophilous plant pollen for zooplankton. Limnol. Oceanogr. **56**: 939–946. doi:10.4319/lo.2011.56.3.0939

Masclaux, H., M. E. Perga, M. Kagami, C. Desvilettes, G. Bourdier, and A. Bec. 2013. How pollen organic matter enters freshwater food webs. Limnol. Oceanogr. **58**: 1185–1195. doi:10.4319/lo.2013.58.4.1185

McCutchan, J. H. J., W. M. J. Lewis, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos **102**: 378–390. doi:10.1034/j.1600-0706.2003.12098.x

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology **48**: 139–149. doi:10.2307/1933425

Orav-Kotta, H., J. Kotta, K. Herkül, I. Kotta, and T. Paalme. 2009. Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* (Amphipoda: Crustacea) in the northern Baltic Sea. Biol. Invasions **11**: 597–608. doi:10.1007/s10530-008-9274-6

Pawlik, M., and D. Ficek. 2016. Pine pollen grains in coastal waters of the Baltic Sea. Oceanol. Hydrobiol. Stud. **45**: 35–41. doi:10.1515/ohs-2016-0004

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models. Can. J. Zool. **92**: 823–835. doi:10.1139/cjz-2014-0127

Pitt, K. A., R. M. Connolly, and T. Meziane. 2009. Stable isotope and fatty acid tracers in energy and nutrient studies of jellyfish: A review. Hydrobiologia **616**: 119–132. doi:10.1007/s10750-008-9581-z

Poisot, T., E. Canard, N. Mouquet, and M. E. Hochberg. 2012. A comparative study of ecological specialization estimators. Methods Ecol. Evol. **3**: 537–544. doi:10.1111/j.2041-210X.2011.00174.x

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. **28**: 289–316. doi:10.1146/annurev.ecolsys.28.1.289

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Reuss, N. S., L. Hamerlik, G. Velle, A. Michelsen, O. Pedersen, and K. P. Brodersen. 2013. Stable isotopes reveal that chironomids occupy several trophic levels within West Greenland lakes: Implications for food web studies. Limnol. Oceanogr. **58**: 1023–1034. doi:10.4319/lo.2013.58.3.1023

Rösel, S., A. Rychła, C. Wurzbacher, and H.-P. Grossart. 2012. Effects of pollen leaching and microbial degradation on organic carbon and nutrient availability in lake water. Aquat. Sci. **74**: 87–99. doi:10.1007/s00027-011-0198-3

Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology **92**: 201–207. doi:10.1890/09-1565.1

Skoog, G. 1978. Influence of natural food items on growth and egg production in brackish water populations of *Lymnea peregra* and *Theodoxus fluviatilis* (Mollusca). Oikos **31**: 340–348. doi:10.2307/3543660

Spiller, D. A., J. Piovia-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. Ecology **91**(5): 1424–1434. https://doi.org/10.1890/09-0715.1

Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ **6**: e5096. doi:10.7717/peerj.5096

Stråät, K. D., C. M. Mörth, A. Sobek, E. Smedberg, and E. Undeman. 2016. Modeling total particulate organic carbon (POC) flows in the Baltic Sea catchment. Biogeochemistry **128**: 51–65. doi:10.1007/s10533-016-0194-8

Swedish Museum of Natural History. 2016. [accessed 2021 June 13th]. Available from https://pollenrapporten.se/prognoser/

stockholm/pollengrafer2016.4.7cdfd911548501e91e52b0e.html

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet δ^{15}N enrichment: A meta-analysis. Oecologia **136**: 169–182. doi:10.1007/s00442-003-1270-z

Wallace, B. J., S. L. Eggert, J. L. Meyer, and J. R. Webster. 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. Ecology **96**: 1213–1228. doi:10.1890/14-1589.1

Ward, E. J., and S. E. Shumway. 2004. Separating the grain from the chaff: Particle selection in suspension- and deposit-feeding bivalves. J. Exp. Mar. Bio. Ecol. **300**: 83–130. doi:10.1016/j.jembe.2004.03.002

Watanabe, K., and T. Kuwae. 2015. How organic carbon derived from multiple sources contributes to carbon sequestration processes in a shallow coastal system? Glob. Chang. Biol. **21**: 2612–2623. doi:10.1111/gcb.12924

Webster, J. R., and J. L. Meyer. 1997. Organic matter budgets for streams: A synthesis. J. N. Am. Benthol. Soc. **16**: 141–161. doi:10.2307/1468247

Zhang, P., B. A. Blonk, R. F. van den Berg, and E. S. Bakker. 2018. The effect of temperature on herbivory by the omnivorous ectotherm snail *Lymnaea stagnalis*. Hydrobiologia **812**: 147–155. doi:10.1007/s10750-016-2891-7

Conflict of Interest

None declared.