Sanderlings Feed on a Diverse Spectrum of Prey Worldwide but Primarily Rely on Brown Shrimp in the Wadden Sea

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Sanderlings feed on a diverse spectrum of prey worldwide but primarily rely on Brown Shrimp in the Wadden Sea

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Knowing what birds eat is fundamental to understand the ecology and distribution of individuals and populations. Often, diet is assessed based on field observations and excrement analyses, which has previously been the case for Sanderling *Calidris alba*. This may have biased their known diets towards large prey with indigestible body parts that can still be recognized in faeces or regurgitations. A literature review of Sanderling diet worldwide showed that Sanderlings exploit a large diversity of prey. We carried out DNA metabarcoding on Sanderling faeces to get a complete view of their diet in the Wadden Sea during staging and moult from late July to early October. Given the diversity of available prey in the Wadden Sea, it was remarkable that 94% of the samples contained Brown Shrimp *Crangon crangon* which, next to the Shore Crab *Carcinus maenas*, were also the most abundant species in the samples. This study shows that whereas Sanderling can feed on a large variety of invertebrates, in the Wadden Sea during southward staging they primarily rely on Brown Shrimp

Key words: DNA metabarcoding, diet composition, *Calidris alba*, shorebirds, *Crangon crangon*, intertidal ecosystems, specialism, foraging behaviour

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Knowing the diet of birds is an essential component of understanding their ecology, behaviour, distribution and population trajectories. Clearly, this also holds for shorebirds (Charadriiformes; Goss-Custard *et al.* 1977, van de Kam *et al.* 2004, Piersma 2012) but knowledge on the diet of coastal sandpipers (Scolopacidae) is undoubtedly incomplete. In sandpipers, the most common methods to assess their diet are focal observations (Sutherland *et al.* 2000, Choi *et al.* 2017) and excrement analyses (Durell & Kelly 1990, Piersma *et al.* 1994, Duijns *et al.* 2013). However, focal observations come with the risk that small or quickly handled prey will remain unnoticed or unidentified (Vanermen *et al.* 2009) and dropping analyses only include species that contain indigestible parts (Dekinga & Piersma 1993). For example, a combination of microscopy of their tongue, isotope analysis and high-resolution filming of foraging behaviour analytical techniques was necessary to discover that Western Sandpipers *Calidris mauri* can graze biofilm (Elner *et al.* 2005, Kuwae *et al.* 2008), which can not be identified as prey using the conventional techniques. Insights from a combination of new techniques may lead to a different view on the ecology of the species in question (Kuwae *et al.* 2012).

Sanderlings *Calidris alba* are also small sandpipers whose diets have been studied mainly by visual observation (Evans *et al.* 1980, Maron & Myers 1985, Masero 2003, Vanermen *et al.* 2009, Grond *et al.* 2015) and microscopic analyses of their faeces (Nuka *et al.* 2005, Castro 2009, Lourenço *et al.* 2015, 2016). Sanderlings inhabit a diverse range of habitats: from freshwater estuaries to coastal beaches in the non-breeding season and High Arctic tundra on the breeding grounds (Reneerkens *et al.* 2009, Conklin *et al.* 2015).

The East Atlantic flyway population of Sanderlings has increased three-fold since the 1980s (van Roomen *et al.* 2018). During that period, peak numbers at the most important staging location in the Dutch Wadden Sea increased even faster, highlighting the increased importance of this area (Loonstra *et al.* 2016). Field observations on the Wadden Sea mudflats suggested that Sanderlings foraged on crustaceans, such as Brown Shrimp *Crangon crangon* (hereafter 'shrimp'; Loonstra *et al.* 2016). However, as in other sandpipers, field observations unlikely give a complete overview of Sanderling diet (Jouta *et al.* 2017). Furthermore, soft-bodied prey will leave little remains in the faeces, making dropping analyses also unsuitable to determine Sanderling diet. Finally, Sanderlings have been reported to regurgitate pellets (Petracci 2002, Kelly 2008), but such pellets are produced considerably less frequently than faeces, and diet reconstructions based on examined pellets will be biased towards prey with indigestible parts (Worrall 1984, Dekinga & Piersma 1993).

We reviewed the scientific literature to get an overview of the Sanderlings' diet worldwide and listed the available (potential) benthic prey of Sanderlings in the Wadden Sea, based on an existing local benthic fauna sampling programme. In addition, we specifically described the diet of Sanderling during southward migration in the Wadden Sea using DNA metabarcoding of the faeces (De Barba *et al.* 2014). This non-invasive method uses the interspecific variation in DNA sequences of a small part of the genome to taxonomically identify prey items, using a reference database (Hebert *et al.* 2003). As such, we can place the diet of Sanderlings in the Wadden Sea into worldwide perspective.

METHODS

Study area

The study was conducted near the uninhabited island Griend (53°14'N, 5°15'E; Figure 1), which is the most important site for Sanderlings in the Dutch Wadden Sea (van den Hout & Piersma 2013). An estimated 11–14% of the flyway population makes use of the Griend area as a staging site (Loonstra *et al.* 2016). Up to 20,000 Sanderlings at one time use the island's beaches to roost (EP pers. obs.). The island is surrounded by extensive mudflats where Sanderlings forage during low tide (van den Hout & Piersma 2013). The area is characterized by a semi-diurnal tide with an amplitude of 1.5–2.5 meters.

Sanderling probing the sediment in search of food. On the intertidal mudflats of the Wadden Sea, Sanderlings predominantly eat shrimp and crabs (photo Jeroen Reneerkens, 15 May 2021).

Literature review

We searched the literature for original papers on Sanderling diet. For each publication, prey species groups and methodology were identified. Additional information was noted on the location, habitat and the season in which the study was carried out. When multiple methods or habitats were used in a study, each was included in our review.

Database of prey items

A list of possible prey items of Sanderlings was constructed based on all species that were found by a large-scale monitoring campaign of intertidal macrofauna that covers the Dutch Wadden Sea (Compton *et al.* 2013). Sediment samples were taken using a sampling corer (25 cm depth and 0.018 m^2 surface) on a 500-m grid with additional random points (Bijleveld *et al.* 2012). For this study, only the 238 sampling points around Griend, which were sampled in July 2018, were included (Figure 1A). Samples were collected during low tide on foot or during high tide from a small boat. Each sample was sieved on a 1-mm mesh sieve and taken back to the NIOZ laboratory to identify all organisms up to species level or the finest taxonomic level possible (Compton *et al.* 2013). The sampling programme detects sedentary species best and likely underestimates mobile species like the Shore Crab *Carcinus maenas* (hereafter 'crab') and shrimp. We considered all benthic species that were encountered on at least five sampling stations, independent of their burying depth, to compile the most generous list of possible prey.

Faecal sample collection

Between late July and early October 2016–2018, we collected faecal samples at 35 locations (Figure 1B). During low tide, flocks of Sanderlings were followed on the mudflat and samples were collected immediately after a group had left the area. To avoid the collection of droppings from other small shorebird species, we collected droppings instantly after a flock had left the area and from flocks consisting of more than 90% Sanderlings only. The samples were picked up with a metal spoon such that we collected as little as possible uric acid (the white part of a dropping) and sediment to avoid deterioration of the DNA and/or contamination of the sample. On each location between 2 and 20 faeces were collected. Each sample was put in a separate plastic bag and stored in the freezer at –10°C within 5 h after collection and remained frozen until DNA extraction. From all the collected samples (n = 310) a random selection of 110 samples was taken for analysis. For one set of samples that was collected at the same time (n = 12), the year and location of collection is known but the day of sampling was lost.

DNA isolation and amplification

DNA was extracted with the Invitrogen PureLink Microbiome DNA Purification Kit, which is especially effective at reducing levels of uric acids, which are present in bird faeces and cause PCR inhibition (Jedlicka *et al.* 2013). Faecal samples were homogenized and subsampled to arrive at a sample weight of <1 g. The sample, together with c. 0.1 g extra 0.1 mm Zircona/Silica beads, was added to a manufacturer-

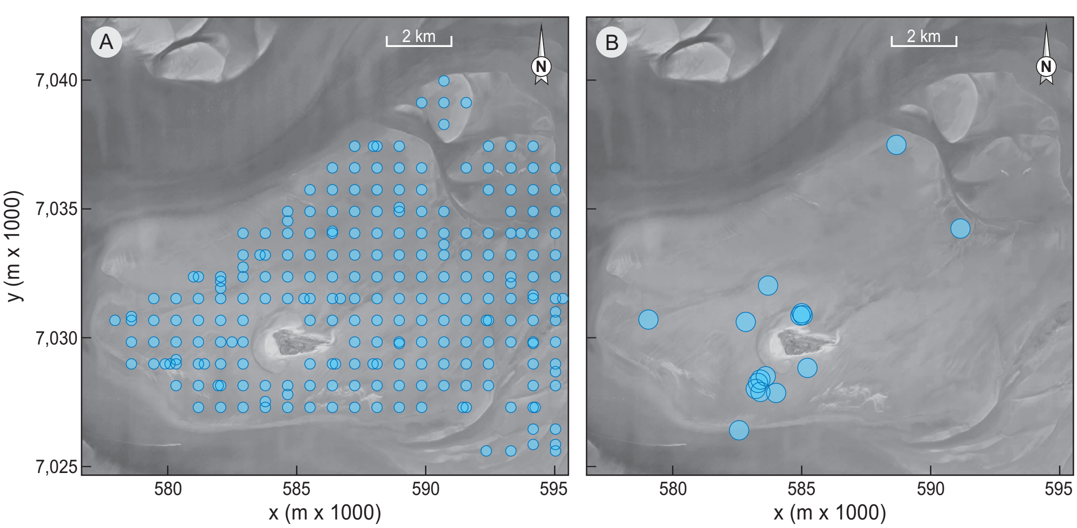

Figure 1. A map of Griend and the surrounding mudflats. (A) Sampling locations on a 500-m grid with additional random points. (B) Locations where faecal samples were collected. Multiple samples were collected per location. The coordinates are in UTM 31N.

provided bead tube and subjected to bead beating in 5×2-min bouts pausing 30 s between bouts. Subsequently the manufacture's protocol was followed. The elution step with 50 μl Ambion purified DNA-free water had an extended incubation time of 4–5 min, and eluted DNA was re-applied to the filter and incubated 2 min extra before final elution.

For PCR amplification AccuStart II PCR ToughMix was used to guarantee amplification success, as the targeted prey DNA may have been degraded. The reaction volume was 10 μl including 5 μl AccuStart, 1μl of each primer (10 μM), 1μl ddH2O and 2μl DNA template. The PCR profile was 3 min at 94°C followed by 35 cycles of 1 min at 94°C, 30 s at 48°C and 1 min at 72°C, and a final extension at 72°C for 10 min. Annealing temperature was set as low as 48°C to minimize taxonomic bias (following Ishii & Fukui 2001). Each sample was amplified in triplicate to avoid initial-cycle template bias. Samples were randomized before DNA extraction and extractions were randomized before PCR. Negative DNA extractions and negative PCR controls were included to track possible contamination of reagents. Before pooling the PCR replicates, 5 μl PCR product was assessed in a standard gel electrophoresis. The 18S rRNA gene was targeted using generic primers SSU-F04 and SSU-R22mod as primer pair with an amplicon length of 450 bp (Sinniger *et al.* 2016, Fonseca *et al.* 2010). Choosing generic primers, we aimed to target the full spectrum of species in Sanderling excrements and limit observation bias. This meant that non-Animalia taxa were also targeted (e.g. Fungi).

DNA sequencing and bioinformatics

PCR products of samples (n = 110), negative extraction controls (n = 3) and PCR controls (n = 4) were sequenced on the MiSeq Sequencer (Illumina) at the Department of Human Genetics, Leiden University Medical Centre, aiming for a read depth of 50,000 per sample. Libraries were prepared with the MiSeq V3 kit, generating 300-bp paired-end reads. The V3-kit does not normalise, which means that it leaves the relative presence of initial PCR product intact, and therefore this library preparation method allows assessing the relative contribution of prey taxa (Verkuil *et al.* 2022).

Low-quality reads with a quality score ≤ 30 over 75% of the nucleotide positions were discarded using the fastq_quality_filter script in the FASTX-Toolkit (http://hannonlab.cshl.edu.fastx_toolkit). The quality filtered reads were front and end clipped to remove the primers. Subsequently, reads were dereplicated and unique reads were discarded. The remaining sequences were clustered in operational taxonomic units (OTUs) using a 98% similarity cut off in VSEARCH (Rognes *et al.* 2016) and singleton OTUs were omitted. The final OTU table was adjusted for the negative extraction controls. Samples were corrected using the nearest extraction control or the mean of two extraction controls for samples that were located between two controls. The sum of all reads in negative extraction controls made up 1.3% of total number of reads (Table S4 and S6). Human DNA, found in negative controls and field samples, made up 0.16% of all reads.

Taxonomic assignments

All OTUs were taxonomically assigned based on a reference database build from the SILVA 18s rRNA database (release 128; Pruesse *et al.* 2007) and our own local Wadden Sea reference database for marine benthic species (GenBank accession numbers MZ709983-MZ710042). OTUs from the taxonomic kingdom of Animalia were identified up to species level or the finest taxonomic level possible. OTUs from other taxa were clustered at the level of phylum or kingdom because we *a priori* rendered it unlikely that these organisms (e.g. Fungi) are part of true Sanderling diet. Taxonomic assignment was performed using the RDP Classifier (Wang *et al.* 2007) with a minimum confidence of 0.8.

Filtering of results

After taxonomic assignment, all non-macrofaunal species groups (i.e. those that are not retained by a 1-mm sieve) were excluded from further analyses. For these species groups it could not be excluded that they ended up in the sample as a result of contamination during sample collection, for example sand containing environmental DNA, or secondary consumption, i.e. prey within the prey on which Sanderlings fed.

Data analyses

The species composition found in the Sanderling faeces was described based on two approaches: frequency of occurrence (presence/absence of taxa) and sequence counts (relative read abundance). The frequency of occurrence is simply the frequency at which a taxon occurred in the samples expressed as a percentage of all samples. The relative read abundance across all samples was calculated by dividing the number of reads of a taxon by the total number of reads. We compared the species composition between faecal samples using the relative read abundance of taxa per sample. The relative read abundances were first Hellinger transformed using function 'decostand' from the vegan package v. 2.5.7 in R (Oksanen *et al.* 2018) followed by the calculation of dissimilarity distances using the Bray-Curtis equation. The resulting dissimilarity matrix was used for analysis of variance species assemblage between (1) sampling locations and (2) month of sampling, using the adonis2 function (permanova) and nonmetric multidimensional scaling (nMDS) plots. Non-metrical dimensional scaling was used to see if the samples from the same location or month of collection were more similar than other samples. The dissimilarity matrix was also used to perform a similarity percentage (Simper) analysis to discriminate between the effect of each species and to answer the question of whether certain species were more important in explaining the variation in a specific time of the year. The relative read abundance of the ten most abundant taxa were calculated per taxa and per sample to show species-specific changes over time. To improve the readability, we fitted a local regression (LOESS function in package ggplot2 v. 3.3.5 (Wickham 2016) to smooth the variation in relative read abundance over time. All statistical data analyses were carried out in R v. 4.1.2 (R Core Team 2021).

RESULTS

Literature overview

We found 28 publications that described Sanderling diet (Table S1) based on behavioural observations, dropping analyses, stable isotope analyses, pellet analyses, stomach content and stomach flushing. Most of the studies used behavioural observations (n = 15) or dropping analysis (n = 9) to determine Sanderling diet. Other non-invasive methods that were used were pellet analysis (n = 2) and DNA metabarcoding of faeces (n = 1) from Arctic breeding grounds. Invasive methods such as stomach flushing (n = 2) and the dissection of Sanderlings to obtain the stomach content (n = 4) were not often applied. Stable isotope analyses of toenails and blood was used in one study. Most studies were carried out in winter and spring (n = 17 and 10, respectively) and along the East Atlantic Flyway (n = 17) and American flyways (n = 11; Figure 2A). Crustaceans and polychaetes were common prey, as well as bivalves, insects, gastropods and fish (Figure 2B). Although Sanderlings have tongue spines that facilitate the consumption of biofilm (Kuwae *et al.* 2012), biofilm turned out to be not of importance in the Sanderling diet (Lourenço *et al.* 2017).

Occurrence of available prey in the Wadden Sea

In 2018, a total of 38 species were found more than five times as part of the sampling programme of benthic fauna in the Wadden Sea (Table S2). Identification up to species level (n = 24) and genus level (n = 9) was most common followed by family (n = 4) and class level (n = 1). Most encountered species around Griend were polychaetes (n = 23), followed by bivalves (n = 8), crustaceans (n = 5) and the Mudsnail *Peringia ulvae* (gastropod).

Metabarcoding

DNA was extracted and amplified from 110 samples collected between 29 July and 6 October in three years

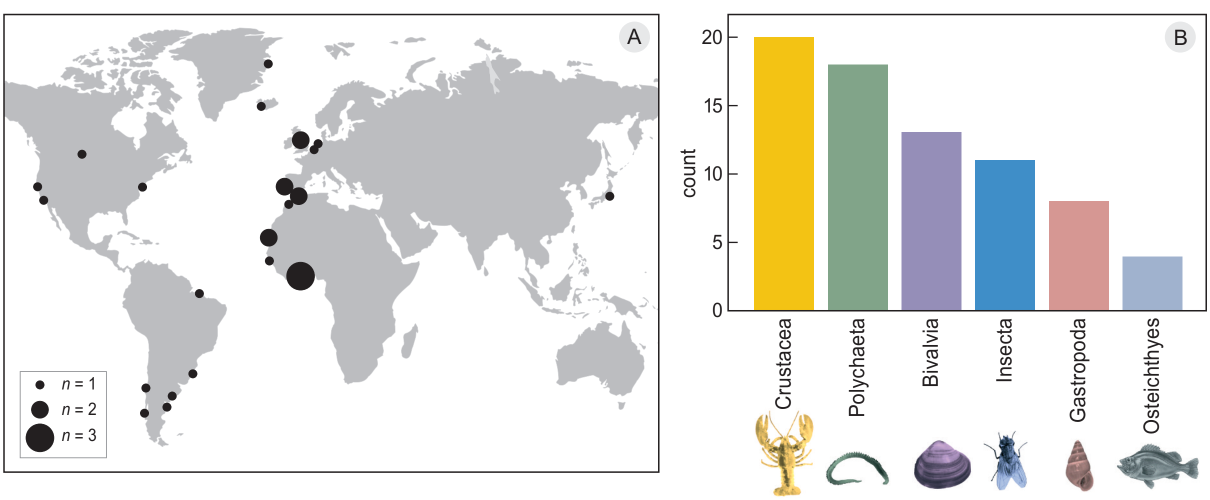

Figure 2. The worldwide diet of Sanderling. (A) World map with the study locations of the reviewed studies. Dot size indicates the number of studies that were conducted. (B) Frequency distribution of prey groups present in examined studies. Only prey groups that occurred in more than two studies are shown. A complete list of Sanderling prey is available in Table S1.

(2016–2018; Table S3), which approximately spans the entire autumn period during which Sanderlings use the Griend area (Loonstra *et al.* 2016). The metabarcoding analysis resulted in 3,258,278 reads (excluding the controls). Raw Illumina sequences were deposited in the European Nucleotide Archive (ENA accession number: PRJEB55071). After clustering and removing 818,566 singletons, 7585 OTUs remained. Taxonomic assignment of these OTUs resulted in 133 different taxa from seven taxonomic kingdoms (all taxa listed in Table S4). The sum of reads in the pooled negative PCR controls (n = 4) was 26 reads with a maximum of 10 per OTU. The sum of reads in the negative extraction controls was 41,922 reads with a maximum of 11,917 reads per OTU. 86% of the reads in the negative extraction controls were of non-macrobenthic taxa. In field samples with DNA template there is a lot of competition for the primers, so very tiny amounts of contaminants would also lead to tiny number of reads. In controls however, the tiniest bit can create many reads. One of the negative extraction control samples contained a very high number of springtail (Collembola) reads (n = 5859, total number of Collembola reads in controls: 5866; Table S6) and another had an exceptionally high number of shrimp reads (n = 79, total number of shrimp reads in controls: 93; Table S6). Therefore, we corrected the number of reads of Collembola and shrimp based on the negative extraction controls (see Table S6 for results of negative controls). In total, 14.6% of all Animalia reads could not be assigned up to species level (Animalia only: 0.09%, Phylum: 0.64% (n = 4), Class: 0.35% (n = 11), Order: 9.39% (n = 28), Family: 0.79% (n = 11), Genus: 3.33% (n = 18)).

Frequency of occurrence

Focusing on macrobenthic species only, we found 47 taxa from five different phyla (see Table S4) in Sanderling excrements. Shrimp were found in 94% of all samples (Figure 3). Another crustacean, Shore Crab, occurred in 91% of all samples, followed by four groups of polychaetes (*Lanice* sp. 84%, Orbiniidae 77%, *Arenicola* sp. 68%, *Hediste* sp. 60%; Figure 3). Twenty-seven of the taxa occurred in less than 10% of the samples. *Scoloplos armiger* was the only species of Orbiniidae found in the sediment cores in our study area. Therefore, Orbiniidae will hereafter be referred to as *Scoloplos armiger*. Similarly, there were only single species of the following genera: *Lanice conchilega*, *Arenicola marina*, *Hediste diversicolor*, *Heteromastus filiformis*, *Eteone longa*, *Mytilus edulis*, *Mya arenaria* and *Ensis leei*. Taxa with unknown Family or lower taxonomic level, will be referred to by their Class: Arachnida (Trombidiformes), Insecta (Diptera).

Relative read abundance

The bulk (97.5%) of all reads originated from ten species (Figure 4) that belonged to the following three phyla: Arthropoda, Annelida and Mollusca (respectively 82.3%, 10.2%, 4.7%). Shrimp were most abun-

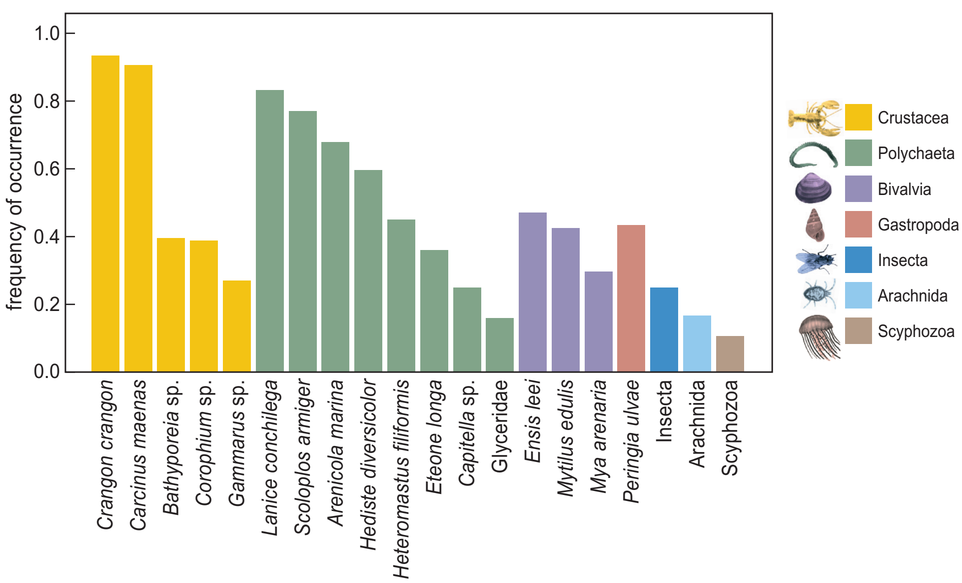

Figure 3. Diet of Sanderlings in the western Dutch Wadden Sea. The frequency of occurrence of taxa that occurred in more than 10% of all samples (n = 20). Taxa were grouped by higher taxonomic levels if possible. Colours refer to the taxonomic class or subphylum (Crustacea). Images of species are chosen to represent higher taxonomic groups.

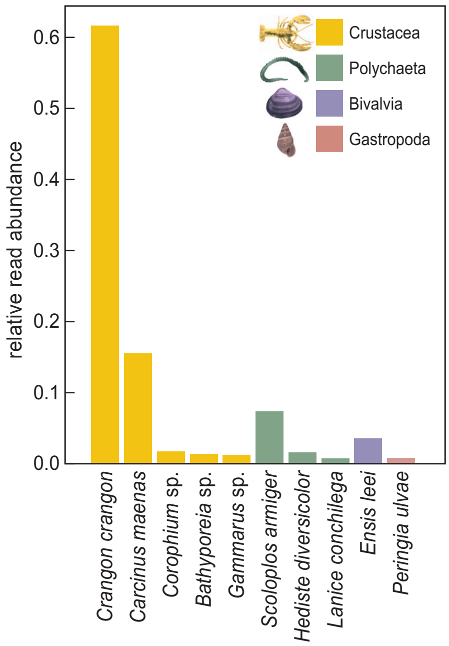

Figure 4. The relative read abundance of the ten most abundant macrobenthic taxa found in the Sanderling diet in the western Dutch Wadden Sea. Each colour refers to a different taxon. Images of species are chosen to represent higher taxonomic groups.

dant and represented 61.7% of all the reads in the samples followed by crabs, Bristle Worms *Scoloplos armiger* and Razor Clams *Ensis leei* (respectively, 15.8%, 7.6%, 3.8%).

Inspection of nMDS plots did not show clear clusters based on either location but suggested differences between months (Figure 5). Permanova analysis confirmed that there was no difference between locations ($F_{1,108}$ = 1.706, P = 0.1), but indicated a significant difference in the diet composition between months ($F_{1,96}$ = 3.278, P = 0.004). The average dissimilarity between months was 54.6% ± 0.02 (SD), with little variation in the dissimilarity between compared months. The lowest dissimilarity was between August and September and the highest dissimilarity was between July and September (Table S5). The greatest difference between months was due to the higher contribution of crab in the diet in July compared to October (Table S5).

We did not detect large seasonal changes in the relative read abundance for different species, except for crabs, whose relative read abundance slightly decreased with the progressing season (Figure 6). Shrimp showed a high relative read abundance throughout the season (Figure 6).

DISCUSSION

Worldwide, Sanderlings exploit a variety of benthic prey: arthropods, gastropods, shellfish, polychaetes and crustaceans. Along the East Atlantic Flyway in which the Wadden Sea is a central wetland, the staple food for Sanderlings wintering in Ghana was the small bivalve *Donax pulchellus* (Grond *et al.* 2015, Quartey 2018). In

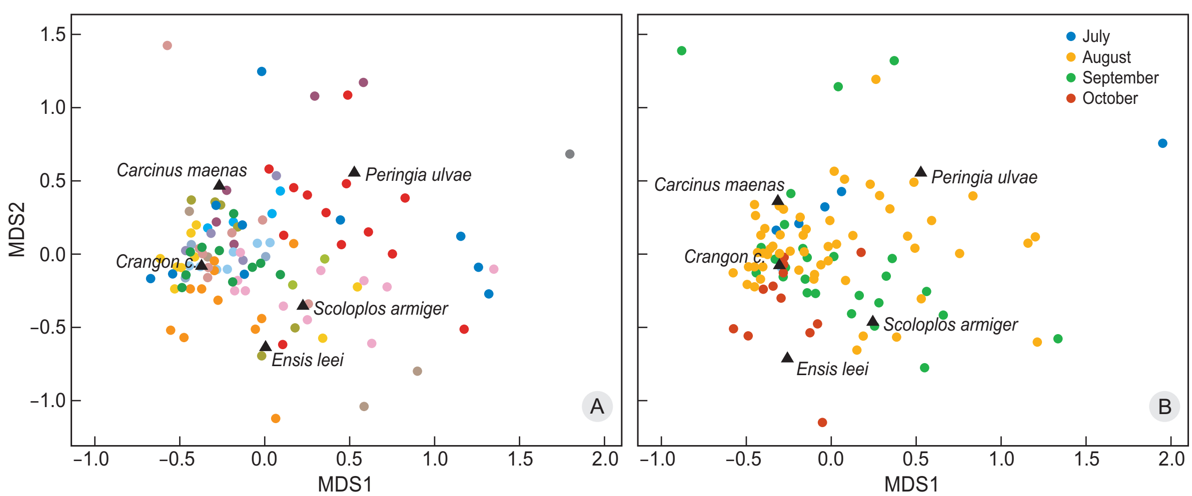

Figure 5. Nonmetric dimensional scaling plots comparing communities in Sanderling faeces. The plots are based on Bray-Curtis dissimilarities of relative read abundance of species within samples for (A) sampling locations and (B) month. Colours represent different sampling location (A) and months (B). Black triangles indicate the position of the five most dominant prey species according to the simper analysis. Small differences in point position are due to differences in sample size (A: n = 110, B: n = 98; see Methods).

Mauritania, Sanderlings foraging on intertidal mudflats mainly ate Mudsnails (Lourenço *et al.* 2016). The diet was complemented with bivalves, polychaetes, crustaceans, insects and to a lesser extent plant material. Sanderlings wintering in Southern Europe had a diet that consisted of bivalves, gastropods, polychaetes and insect larvae (Perez-Hurtado *et al.* 1997, Masero 2003, Lourenço *et al.* 2015). On Belgian shores, Sanderlings ate a variety of prey, of which the polychaete *Scolelepis squamata* and the flesh of dead bivalves or those that were washed up ashore were important components (Vanermen *et al.* 2009). On Dutch beaches Sanderlings mainly fed on *Scolelepis squamata* in winter (Grond *et al.* 2015). Like most other Arctic-breeding shorebirds, Sanderlings ate arthropods on the breeding grounds (Wirta *et al.* 2015, Reneerkens *et al.* 2016).

Given that species from all taxa commonly consumed by Sanderlings were present in the Wadden Sea, it is striking that DNA metabarcoding revealed a predominance of shrimp in Sanderling faeces (94% of the samples). The shrimp showed a steady presence in the diet throughout the entire season of southward migration. In terms of the number of sequence reads, shrimp were also the most abundant species (61.8% of all reads). Crabs occurred in 91% of the samples and were the second most common and abundant species with 15.8% of all reads. Perhaps surprisingly, shrimp and, to a lesser extent, crabs, did not frequently occur in the benthic sampling program (Table S2), but we believe that this is because mobile species such as shrimp and crabs, can escape before the sample is taken. We did not detect an effect of sampling location

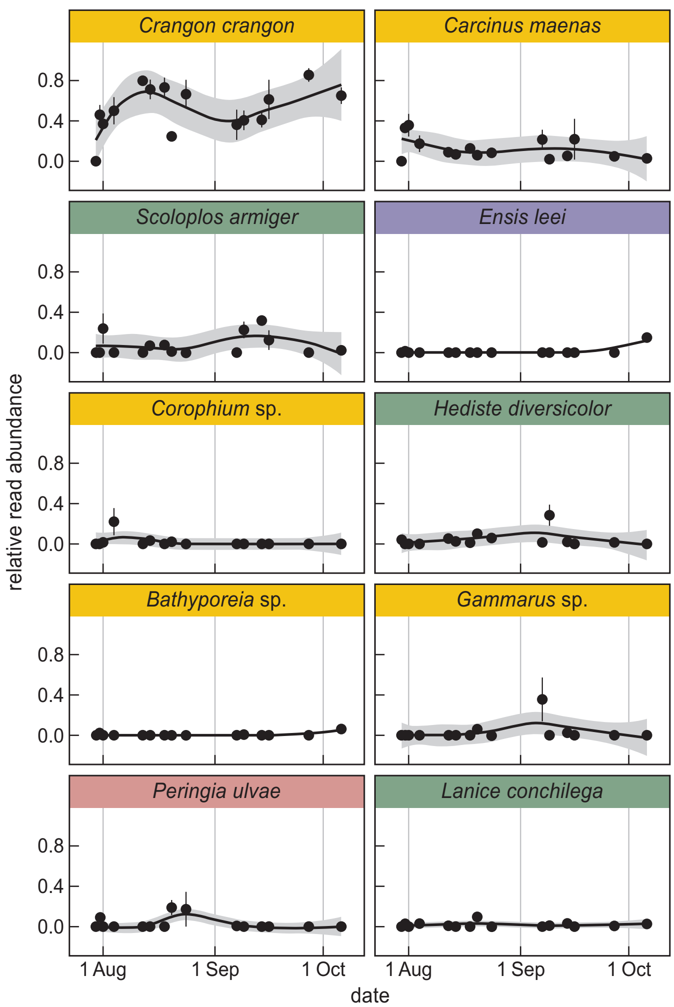

Figure 6. The relative read abundance per species per sample over time. Dots indicate the means, bars the SE and the black line is the LOESS smoothed mean (span = 0.75) with 95% CI (grey). The colours of the banners refer to the taxonomic class in correspondence with Figures 2–4.

on Sanderling diet composition, so the diet was similar across the sampling locations. Even though shrimp and crabs were by far the most important prey for Sanderlings in the Wadden Sea, these species have only been described as Sanderling prey species in the Wash in England (Kelly 2008), an intertidal area close to and quite similar to the Wadden Sea (Bocher *et al.* 2007).

Why do Sanderlings in the Wadden Sea eat shrimp and crabs? Shrimp and crabs are relatively soft-bodied prey, which are easy to digest compared with hard-bodied prey such as bivalves and gastropods (van Gils *et al.* 2003). Hard-bodied prey forces birds to take digestive breaks, leaving less time for foraging (van Gils *et al.* 2005a). Sanderlings ingesting whole bivalves in Ghana indeed spent a lot of time seemingly inactive, presumably to process the shell material (Grond *et al.* 2015). Therefore, in terms of digestibility, shrimp and crabs could be a more profitable prey because they contain little indigestible ballast mass compared to bivalves (van Gils *et al.* 2005b). In addition to that, shorebirds that forage on hard-bodied prey need to maintain a larger gizzard to crush the shell material (Dekinga *et al.* 2001, Piersma *et al.* 1993). Considering that a significant proportion of the Sanderling population in our study area was fuelling up for migration (Loonstra *et al.* 2016), foraging on hard-bodied prey, which would involve the carrying of a heavy organ, would not be favourable (Piersma 1998).

Furthermore, Brown Shrimp are rich in polyunsaturated fatty acids, specifically docosahexaenoic acid (C22:6n-3) and eicosapentaenoic acid (C20:5n-3; Mika *et al.* 2012 & Turan *et al.* 2012), which were shown to be quickly incorporated into body lipids and to increase the activity of flight muscle enzymes important for prolonged flight (Maillet & Weber 2006). For that reason, it may be that shrimp are a very suitable prey for Sanderlings prior to migration. Still, levels of polyunsaturated fatty acids are lower in autumn (when Sanderlings stage in the Wadden Sea) and in juveniles (the age group eaten by Sanderlings) and specific values for the Wadden Sea are unknown so further research is required to determine the nutritional value of shrimp for Sanderlings (Moore 1976, Mika *et al.* 2014).

Shrimp that occur on mudflats are mostly juveniles that leave the intertidal to become adults in the subtidal (Tiews 1970). The young shrimp rapidly disappear from mudflats from August onwards (Beukema 1992). Small shrimp (<20 mm) were swallowed whole by Sanderlings while the scarcer large shrimp (>20 mm) were stabbed and only their flesh was picked out (EP & JR pers. obs.). This implies that all sizes of shrimp may be edible for Sanderlings, which could explain the high relative read abundance of shrimp throughout the study period (Figure 6). Still, there may be differences in profitability for shrimp of different sizes. Large shrimp may be more difficult to catch for Sanderlings compared to small shrimp, while the gain in terms of flesh mass is higher. Foraging experiments with captive Sanderlings that are fed with different-sized shrimp could reveal whether such a trade-off exists.

The importance of crabs in the Sanderling diet decreased over the season (Figure 6), contributing to the slight change in diet composition across months, according to the simper analysis. Like shrimp, crabs decrease in abundance after July and they reach larger sizes (Beukema 1991, van Gils *et al.* 2005b). Large crabs (>20mm) are less common on mudflats than small crabs (<20 mm; Beukema 1991) and like large shrimp, probably require more handling time. Moreover, the strength of the crab carapace may not allow to be opened by a Sanderling bill at all. Therefore, Sanderlings foraged mainly on small crabs (EP pers. obs). As crabs were mostly swallowed whole by Sanderlings, at some point they may have outgrown the edible size for Sanderlings (Zwarts & Blomert 1992).

Most encountered species by the benthic sampling program were polychaetes. Still, not many polychaetes were common or abundant in the Sanderling diet, possibly because they were buried deeper than 2 cm and therefore unavailable for Sanderlings (Gerritsen & Meiboom 1986). *Scoloplos armiger* was the only taxon of polychaetes that was both common and abundant in their diet. An average *Scoloplos armiger* contains 0.004 g ash free dry mass (Duijns *et al.* 2013). This is 3–4 times less than the biomass of an average sized shrimp or crab from the mudflat (respectively 0.011 g and 0.014 g; Duijns *et al.* 2013, Zwarts & Wanink 1993). In order to obtain the same energy uptake, Sanderlings would therefore need to eat 3 to 4 times more *Scoloplos armiger* compared to shrimp or crabs. Prey density had the largest effect on the intake rate of Sanderlings at a beach along the Pacific coast of California, USA (Myers *et al.* 1980). To learn more about the profitability of a Wadden Sea prey, we would need information on prey density as well as handling times of specific prey items to compare the functional responses of Sanderling foraging on different prey items.

Razor clams *Ensis* spp. have been described as prey for Sanderlings in winter (Vanermen *et al.* 2009); Sanderlings picked out the meat from clams that stranded on beaches (Kelly 2008). In our results, the importance of razor clams in the diet increased in

October due to a single sample (Figure 6). Perhaps, an increased storm frequency in this time of year lead to strandings of razor clams on mudflats, which could serve as food for Sanderlings. Interestingly, the contribution of prey that were not shrimp or crab, remained relatively stable over the season (Figure 6). It may be that Sanderlings miss out on specific nutrients by foraging exclusively on shrimp and crab. Therefore Sanderlings, like other vertebrate carnivores, may selectively forage on other prey to balance their diet (Kohl *et al.* 2005).

Biofilm is part of the diet of North American Western Sandpipers, but Lourenço *et al.* (2017) found that biofilm was not of importance in the Sanderling diet. Even though this study was conducted on wintering grounds and on more southern latitudes, there are good reasons to extend their conclusions to the Wadden Sea. First, the biofilm mats that other smaller shorebirds use to forage on elsewhere (Elner *et al.* 2005), do not occur in the places where we observed Sanderlings foraging and where faecal samples were collected in the Wadden Sea. The water and sand dynamics in our study area are probably too high for substantial biofilm to develop. Secondly, we did not observe foraging behaviour that is associated with eating biofilm while we did observe Sanderlings eating shrimp and crabs. The searching behaviour of Sanderlings was characterized by relatively few probes in the sediment, moving fast through the habitat, switching often between movements with the bill pointing to the ground and standing up straight, then turning the head and body to follow the moving prey (EP pers. obs). For Sanderlings to obtain enough meiofauna or biofilm, we expected to see foraging behaviour that matches those prey types. Western Sandpipers foraging on meiofauna showed a high frequency pecking mode and slow movement through the habitat (Kuwae *et al.* 2008), which we did not observe in Sanderlings on mudflats in our study area.

Over the past decades, shrimp have become more abundant during the spring staging period of Sanderlings (May) in the Wadden Sea (Penning *et al.* 2021). It is unknown whether the availability of shrimp has also increased during the autumn staging period. Sanderlings use the Wadden Sea to fuel up during northward and southward migration and as such, the availability of benthic prey on the intertidal mudflats are important for a significant part of the East Atlantic Flyway population of Sanderlings (Loonstra *et al.* 2016). Sanderlings wintering in Africa use multiple staging sites during northward migration, of which the longest time is used for re-fuelling in the Wadden Sea compared with more southerly locations (Reneerkens *et al.* 2020). This suggests that a large proportion of the flyway population fuels up predominantly preying on shrimp. Perhaps, the (current) presence of large densities of shrimp and crabs make the Wadden Sea a more suitable staging site than more southerly wetlands along the flyway. It is currently unknown to what extent changes in shrimp abundance have affected the local and flyway-wide population growth of Sanderlings.

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SAMENVATTING

Voor een beter begrip van de ecologie en verspreiding van vogels is kennis van hun voedsel fundamenteel. In de meeste studies wordt het voedsel bepaald aan de hand van veldobservaties en analyses van uitwerpselen. Dat is ook bij Drieteenstrandlopers *Calidris alba* het geval. Het is daardoor mogelijk dat we een vertekend beeld hebben van de prooikeuze, doordat voornamelijk grote prooien met onverteerbare delen herkend kunnen worden in de uitwerpselen of braakballen. Een literatuuroverzicht van wereldwijde onderzoeken naar het voedsel van Drieteenstrandlopers liet zien dat deze strandlopers een grote diversiteit aan prooisoorten benutten. Met behulp van DNA metabarcoding van uitwerpselen van Drieteenstrandlopers hebben we het volledige menu van in de nazomer in de Waddenzee opvettende en ruiende Drieteenstrandlopers in kaart gebracht. Gezien de grote diversiteit aan aanwezige prooisoorten in de Waddenzee was het opmerkelijk dat 94% van de monsters de Gewone Garnaal *Crangon crangon* bevatte. Gewone Garnalen waren naast de Strandkrab *Carcinus maenas* bovendien het meest talrijk in de verzamelde uitwerpselen. Hoewel Drieteenstrandlopers zich dus kunnen voeden met een grote diversiteit aan evertebraten, benutten ze in de Waddenzee tijdens de zuidwaartse trek voornamelijk de Gewone Garnaal.

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SUPPLEMENTARY MATERIAL

Table S1. Summary of the 28 studies on Sanderling that were reviewed. Per study, species were sorted on a higher taxonomic level if possible. Horizontal lines separate studies and within studies lines separate method, location, habitat or season.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Polychaeta	*Hediste diversicolor*	++	stomach flushing	Vignisson 2019	Iceland	Reykjanesskagi	sandy beach or wrack beds	spring	EAF	64°N
	Capitella capitata	++								
	Spirorbis sp.	+								
Oligochaeta	unidentified	++								
Crustacea	*Amphipoda* sp.	+								
Gastropoda	unidentified	+								
Insecta	*Coelopa frigida* (Fly)	+++								
	Coelopa frigida (Larvae)	+++								
Foraminifera	unidentified	++								
Briozoa	unidentified	+								
Insecta	*Platymischus dilatatus*	+								
Coleoptera	*Micralymma marinum*	+								
	Micralymma marinum	+	stomach and intestine content							
Insecta	*Diptera* sp.	++								
Polychaeta	unidentified	+++								
	Spirorbis sp.	+								
	Hediste diversicolor	++								
Crustacea	*Amphipoda* sp.	+								
Pycnagonida	*Pycnogonum litorale*	+								
Briozoa	unidentified	+								
Plastic	unidentified	+								
Foraminifera	unidentified	+								
Gastropoda	unidentified	++								
Gastropoda	*Hydrobia ulvae*	++	dropping analysis	Lourenço *et al.* 2015	Portugal	Tejo	estuarine muddy sand	winter	EAF	38°N
Bivalvia	*Scrobicularia plana*	++								
Crustacea	*Cyathura carinata*	+								
Insecta	*Staphylinidae* sp.	+++					estuarine sandy beach			
Gastropoda	*Hydrobia ulvae*	++								
Polychaeta	unidentified	++								
Bivalvia	*Scrobicularia plana*	+								
	Cerastoderma edule	+								
Crustacea	*Cyathura carinata*	+								

Table 1. Continued.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Insecta	*Chironomid larvae*	+++			Portugal	Oeiras and Caparica	rocky intertidal			
Bivalvia	*Mytilus galloprovincialis*	++								
	Donax trunculus	+								
Gastropoda	*Melaraphe neritoides*	+								
Bivalvia	*Mytilus galloprovincialis*	+					sandy coast			
	Donax trunculus	++								
Polychaeta	*Nephtys hombergii*	+								
	Sedent. polychaetes	+								
Insecta	Chironomid larvae	+								
	Staphylinidae sp.	+								
Gastropoda	*Hydrobia ulvae*	++	dropping analysis	Lourenço *et al.* 2016	Mauritania	Banc d'Arguin	intertidal mudflats and sandy coast	winter	EAF	19°N
Bivalvia	*Dosinia isocardia*	+								
Polychaeta	mainly sedent. polychaetes and *Nereis* sp.	++								
Crustacea	mainly amphipoda and anthuridae	++								
Insecta	*Staphylinidae* sp.	++								
plant fragments		+								
macro-invertebrates		+++	stable isotopes	Lourenço *et al.* 2017	Portugal	Tejo	intertidal mudflats and saltpans	winter	EAF	38°N
biofilm		+								
microbenthos		x								
macro-invertebrates		+++			Morocco	Sidi Moussa	intertidal mudflats and saltpans			32°N
biofilm		+								
microbenthos		x								
macro-invertebrates		+++			Mauritania	Banc d'Arguin	intertidal mudflats and sandy coast			19°N
biofilm		+								
microbenthos		x								
macro-invertebrates		+++			Guinea-Bissau	Bijagós Archipelago	intertidal mudflats and sandy coast			11°N
biofilm		+								
microbenthos		x								

Table 1. Continued.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Gastropoda		+	beh. obs.	Perez-Hurtado *et al.* 1997	Spain	Cádiz	sandy coast	winter	EAF	36°N
Bivalvia		+								
Polychaeta		+								
Polychaeta	unidentified		beh. obs.	Masero 2003	Spain	Guadalete River	intertidal mudflat	winter	EAF	36°N
Crustacea	*Artemia* sp.					Cádiz Bay	salt pans			
Polychaeta	*Nephtys* sp.		beh. obs.	Kelly 2008	UK		intertidal mudflat	unsp.	EAF	52°N
	Scolelepis squamata									
Crustacea	*Crangon crangon*									
	Crab sp.									
	Bathyporeia sp.									
	Corophium volutator									
	Talitrus saltator									
	Eurydice pulchra									
Gastropoda	*Hydrobia* sp.									
Insecta	unidentified									
macroalgae	seaweed									
Cnidaria	*Aurelia aurita*									
Bivalvia	*Ensis* sp.									
	Cerastoderma edule		pellet analysis							
	Limecola balthica									
Polychaeta	*Nerine cirratus*		beh. obs.	Evans *et al.* 1980	UK	Teesmouth	sandy coast	unsp.	EAF	54°N
Crustacea	*Eurydice pulchra*									
	Bathyporeia sp.									
Polychaeta	unidentified	+++	beh. obs.	Vanermen *et al.* 2009	Belgium	coast	sandy coast	winter	EAF	51°N
Bivalvia	*Mytilus edulis*	+								
	Donax vittatus	+								
	Ensis sp.	++								
Crustacea	unidentified	+								
Cnidaria	Anemones	+								
Crustacea	*Crangon crangon*	+++	beh. obs.	Loonstra *et al.* 2016	NL	Griend	intertidal mudflat	autumn	EAF	53°N
Arthropoda		+++	DNA metabarcoding	Wirta *et al.* 2015	Greenland	Zackenberg	high arctic tundra	summer	EAF	74°N
Invertebrates	soft-bodied invertebrates	+++	beh. obs.	Ntiamoa-Baidu *et al.* 1998	Ghana	Songor and Keta Lagoon	brackish water lagoon	winter	EAF	5°N

Table 1. Continued.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Ruppiaceae	*Ruppia maritima* seeds		dropping analysis and beh. obs.	Piersma & Ntiamoa-Baidu 1995	Ghana	Songor and Keta Lagoon	brackish water lagoon	winter	EAF	5°N
Osteichthyes	fish remains									
	larval fish									
Crustacea	*Amphipoda* sp.									
Polychaeta	unidentified									
Polychaeta	unidentified	++	beh. obs.	Grond *et al.* 2015	NL	Vlieland	sandy coast	autumn	EAF	53°N
unknown	unidentifiable prey items	+++								
Bivalvia	*Donax pulchellus*	+++			Ghana	Esiama		winter	EAF	5°N
Bivalvia	*Donax* sp.	+++	beh. obs.	Reneerkens *et al.* 2009	Ghana	Esiama	sandy coast	winter	EAF	5°N
Bivalvia	*Donax pulchellus*	+++	dropping analysis	Quartey 2018	Ghana	Esiama	sandy coast	winter	EAF	5°N
Polychaeta	*Excirolana chiltoni*	++								
	Glycera sp.	+								
Gastropoda	*Hastula aciculina*	+								
Osteichthyes	Fish sp.	+								
Bivalvia	*Donax semigranosus*	++	dropping analysis	Nuka *et al.* 2005	Japan	Kujukuri Beach	sandy coast	au-wi	EAAF	35°N
Crustacea	*Excirolana chiltoni*	++								
	Archaeomysis vulgaris	++								
Insecta	unidentified	++								
Polychaeta	*Nereidae* sp.	+	dropping analysis	Petracci 2002	Argentina	Monte Hermoso	sandy coast	winter	AF	38°S
Bivalvia	*Brachydontes rodriguezi*	++								
	Corbula sp.	+								
Crustacea	*Corophium* sp.	++								
Insecta	*Coleoptera* sp.	++								
	Diptera sp.	++								
Osteichthyes	*Perciformes* sp.	+								
Bivalvia	*Brachydontes rodriguezi*	+++	pellet analysis							
	Corbula sp.	++								
Insecta	*Coleoptera* sp.	+++								
	Diptera sp.	+								
	Formicidae sp.	+								
Crustacea	*Corophium* sp.		beh. obs.							
Polychaeta	*Nereidae* sp.									
	Glycera sp.									
	green algae									

Table 1. Continued.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Polychaeta	unidentified		beh. obs.	Harrington *et al.* 1986	Brazil	Lagoa do Peixe	sandy coast	winter	AF	31°S
Crustacea	*Emerita* sp.									
Polychaeta	*Malacoceros glutaes*	+	stomach content	Sallaberry *et al.* 1996	Chile	Roquant Island	sandy coast	winter	AF	36°S
	Perinareis vallata	++								
	Scolelepis squamata	+								
Crustacea	*Cancer setosus*	+++								
	Emerita analoga	+								
	Exirolana hirsuticauda	+								
	Lepidopa chilensis	+								
Insecta	*Carabidae* sp.	+								
	Coleoptera sp.	++								
	Ligacidae sp.	+								
Bivalvia	*Aulacomya ater*	+								
	Mulinia edulis	++								
	Semimytilus algos	+								
Gastropoda	*Littorina araucana*	+								
	Nassarius gayi	+								
Crustacea	*Corophium* sp.		beh. obs.	Myers 1980	USA	Abbott's Lagoon	sandy coast	winter	AF	38°N
	Anisogammarus sp.									
Crustacea	*Orchestoidea tuberculata*	+	dropping analysis	Castro *et al.* 2009	Chile	Isla Guamblin	sandy coast	winter	AF	44°S
Bivalvia	*Mesodesma donacium*	++								
Insecta	*Phalerisida maculata*	+++								
Limulidae	*Limulus polyphemus*	+++	stomach flushing	Tsipoura and Burger 1999	USA	Delaware Bay	sandy coast	spring	AF	39°N
Polychaeta	*Capitellidae* sp.	++								
	Spionidae sp.	++								
Insecta	*Diptera* sp.	+								
Nemertea	*Lineus* sp.	+								
Osteichthyes	fish remains	+								
Crustacea	*Emerita analoga*	++	beh. obs.	Maron and Myers 1985	USA	Bodega Ba	sandy coast	autumn	AF	38°N
Polychaeta	*Excirolana linguifrons*	+								
	other	++								

Table 1. Continued.

Taxon*	Species	FOO**	Method	Reference	Country	Location	Habitat	Season	Flyway***	Latitude
Crustacea	*Emerita analoga*	+						winter		
Polychaeta	*Excirolana linguifrons*	++								
	other	++								
Crustacea	*Emerita analoga*	++						spring		
Polychaeta	*Excirolana linguifrons*	+								
	other	+								
Bivalvia	unidentified	++	beh. obs.	Kober and Bairlein 2006	Brazil	Bragantinian Peninsula	intertidal mudflat and sandy coast	spring	AF	00°N
Gastropoda	unidentified	+								
Polychaeta	unidentified	++								
Bivalvia	*Tellina* sp.		dropping analysis							
Crustacea	*Callianassidae* sp.									
Polychaeta	*Nereidae* sp.									
	Spionidae sp.									
Crustacea	*Emerita analoga*	+++	stomach content	Reeder 1951	USA	Point Mugu	sandy coast	spring	AF	34°N
Crustacea	*Artemia salina*		stomach content	Alexander 1994	Canada	Chaplin Lake	saline lake	spring	AF	50°N
	Ephydra sp.									
Crustacea	*Exosphaeroma* sp.	+++	dropping analysis	Hernández & Bala 2005	Argentina	Punta Norte	rocky beach	spring	AF	42°S
Crustacea	*Cyrtograpsus affinis*	++								
	Isopoda sp.	++								
Polychaeta	*Laeonereis acuta*	++								
Insecta	unidentified	+								

*Taxons are not consistently referring to the same taxonomic level.
**Frequency of occurrence: +++ = >50% ++ >10% + = <10%.
***EAF = East Atlantic Flyway, EAAF = East Asian-Australasian Flyway, AF = American Flyways.

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Table S2. List of species that were encountered more than five times by the benthic sampling programme near Griend. Counts refer to the number of times the species was encountered. Species are sorted by count within Class or in the case of Crustacea, by sub-phylum (separated by horizontal lines).

Species	Taxon	Count
Limecola balthica	Bivalvia	150
Mya arenaria	Bivalvia	108
Cerastoderma edule	Bivalvia	98
Ensis leei	Bivalvia	91
Abra tenuis	Bivalvia	47
Mytilus edulis	Bivalvia	13
Kurtiella bidentata	Bivalvia	9
Macomangulus tenuis	Bivalvia	6
Urothoe sp.	Crustacea	79
Corophiidae	Crustacea	59
Carcinus maenas	Crustacea	43
Bathyporeia sp.	Crustacea	15
Crangon crangon	Crustacea	15
Peringia ulvae	Gastropoda	70
Scoloplos armiger	Polychaeta	196
Eteone longa	Polychaeta	194
Pygospio elegans	Polychaeta	184
Capitella sp.	Polychaeta	171
Marenzelleria viridis	Polychaeta	170
Hediste diversicolor	Polychaeta	151
Phyllodoce mucosa	Polychaeta	146
Heteromastus filiformis	Polychaeta	124
Oligochaeta	Polychaeta	119
Arenicola marina	Polychaeta	117
Nereididae	Polychaeta	56
Cirratulidae	Polychaeta	55
Lanice conchilega	Polychaeta	50
Polydora sp.	Polychaeta	30
Nephtys sp.	Polychaeta	24
Polynoidae	Polychaeta	10
Eunereis longissima	Polychaeta	9
Alitta succinea	Polychaeta	8
Magelona sp.	Polychaeta	8
Scolelepis sp.	Polychaeta	7
Spio sp.	Polychaeta	6
Spiophanes bombyx	Polychaeta	6
Lagis koreni	Polychaeta	5

Table S3. Date and location of the collected faecal samples.

Date	*n*	Latitude (°N)	Longitude (°E)
30 July 2016	1	53.2339	5.2335
1 August 2016	6	53.2424	5.2394
4 August 2016	3	53.2453	5.2426
4 August 2016	4	53.2446	5.2408
18 August 2016	5	53.2760	5.3106
14 September 2016	2	53.2642	5.2434
16 September 2016	5	53.2438	5.2401
27 September 2016	4	53.2935	5.28835
31 July 2017	4	53.2582	5.2552
12 August 2017	10	53.2417	5.2462
14 August 2017	11	53.2420	5.2409
20 August 2017	13	53.2578	5.2554
24 August 2017	4	53.2469	5.2572
7 September 2017	5	53.2579	5.2547
9 September 2017	11	53.2564	5.2357
2017	12	NA	NA
6 October 2018	12	53.2569	5.2018

Table S4. Taxa detected by DNA barcoding of Sanderling excrements. Bold cells mark the macrobenthic species that were included in the study. 'Total reads' indicates the sum of the number of reads of all samples. FOO is the frequency of occurrence.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Total reads	FOO
Animalia	Annelida	Clitella	Haplotaxida				170	0.118
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Glyceridae**			**420**	**0.164**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Nephtyidae**	**Nephtys**		**9**	**0.027**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Nereididae**	**Alitta**	**succinea**	**111**	**0.018**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Nereididae**	**Alitta**	**virens**	**5**	**0.009**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Nereididae**	**Hediste**		**8195**	**0.600**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Phyllodocidae**	**Eteone**		**1404**	**0.364**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Phyllodocidae**	**Phyllodoce**		**23**	**0.036**
Animalia	**Annelida**	**Polychaeta**	**Phyllodocida**	**Polynoidae**	**Bylgides**		**41**	**0.027**
Animalia	**Annelida**	**Polychaeta**	**Spionida**	**Spionida**			**37**	**0.064**
Animalia	**Annelida**	**Polychaeta**	**Spionida**	**Spionidae**	**Malacoceros**	**fuliginosus**	**16**	**0.055**
Animalia	**Annelida**	**Polychaeta**	**Spionida**	**Spionidae**	**Marenzelleria**	**viridis**	**120**	**0.082**
Animalia	**Annelida**	**Polychaeta**	**Spionida**	**Spionidae**	**Spio**		**372**	**0.091**
Animalia	**Annelida**	**Polychaeta**	**Terebellida**	**Pectinariidae**	**Lagis**	**koreni**	**7**	**0.018**
Animalia	**Annelida**	**Polychaeta**	**Terebellida**	**Terebellida**	**Lanice**		**4409**	**0.836**
Animalia	**Annelida**	**Polychaeta**		**Arenicolidae**	**Arenicola**		**2797**	**0.682**
Animalia	**Annelida**	**Polychaeta**		**Capitellidae**	**Capitella**		**1667**	**0.255**
Animalia	**Annelida**	**Polychaeta**		**Capitellidae**	**Heteromastus**		**667**	**0.455**
Animalia	**Annelida**	**Polychaeta**		**Orbiniidae**			**35126**	**0.773**
Animalia	**Annelida**	**Polychaeta**					59	0.164
Animalia	Annelida						52	0.036
Animalia	**Arthropoda**	**Arachnida**	**Trombidiformes**				**1117**	**0.173**
Animalia	**Arthropoda**	**Collembola**					**65**	**0.027**
Animalia	Arthropoda	Hexanauplia	Calanoida	Acartiidae	Acartia	bifilosa	483	0.091
Animalia	Arthropoda	Hexanauplia	Calanoida	Centropagidae	Centropagus	typicus	9	0.009
Animalia	Arthropoda	Hexanauplia	Calanoida	Temoridae	Temora	longicornis	32	0.045
Animalia	Arthropoda	Hexanauplia	Calanoida				37	0.018
Animalia	Arthropoda	Hexanauplia	Cyclopoida	Oithonidae	Oithona	davisae	4	0.018
Animalia	Arthropoda	Hexanauplia	Cyclopoida				16	0.018
Animalia	Arthropoda	Hexanauplia	Harpacticoida	Ameiridae	Ameira	scotti	20	0.027
Animalia	Arthropoda	Hexanauplia	Harpacticoida	Ectinosomatidae	Bradya		120	0.118
Animalia	Arthropoda	Hexanauplia	Harpacticoida	Harpacticidae	Harpacticus		67133	0.936
Animalia	Arthropoda	Hexanauplia	Harpacticoida				10179	0.864
Animalia	Arthropoda	Hexanauplia	Sessilia				47	0.018
Animalia	Arthropoda	Hexanauplia					1212	0.355

Table S4. Continued.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Total reads	FOO
Animalia	**Arthropoda**	**Insecta**	**Coleoptera**				**38**	**0.027**
Animalia	**Arthropoda**	**Insecta**	**Diptera**				**1475**	**0.255**
Animalia	**Arthropoda**	**Insecta**	**Hymenoptera**				**42**	**0.018**
Animalia	**Arthropoda**	**Insecta**	**Siphonaptera**				**15**	**0.018**
Animalia	**Arthropoda**	**Malacostraca**	**Amphipoda**	**Corophiidae**	**Corophium**		**8953**	**0.391**
Animalia	**Arthropoda**	**Malacostraca**	**Amphipoda**	**Gammaroidae**	**Bathyporeia**		**7417**	**0.400**
Animalia	**Arthropoda**	**Malacostraca**	**Amphipoda**	**Gammaroidae**	**Gammarus**		**6330**	**0.273**
Animalia	**Arthropoda**	**Malacostraca**	**Amphipoda**	**Melitidae**	**Melita**		**12**	**0.009**
Animalia	**Arthropoda**	**Malacostraca**	**Decapoda**	**Carcinidae**	**Carcinus**	**maenas**	**72690**	**0.909**
Animalia	**Arthropoda**	**Malacostraca**	**Decapoda**	**Crangonidae**	**Crangon**	**crangon**	**284226**	**0.936**
Animalia	Arthropoda	Malacostraca	Decapoda				3362	0.700
Animalia	**Arthropoda**	**Malacostraca**	**Mysida**	**Mysidae**	**Gastrosaccus**	**spinifer**	**4**	**0.009**
Animalia	**Arthropoda**	**Malacostraca**	**Mysida**	**Mysidae**	**Praunus**	**flexuosus**	**14**	**0.018**
Animalia	Arthropoda	Malacostraca	Mysida				96	0.045
Animalia	Arthropoda	Malacostraca					14	0.009
Animalia	Arthropoda	Ostracoda	Podocopida	Cytheruridae	Semicytherura	striata	2653	0.391
Animalia	Arthropoda	Ostracoda	Podocopida				195757	0.964
Animalia	Arthropoda						94	0.018
Animalia	Aves						15302	0.918
Animalia	Chordata	Actinopterygii					4433	0.327
Animalia	Chordata	Appendicularia	Copelata	Oikopleuridae			141	0.118
Animalia	Chordata	Ascidiacea	Stolidobranchia				104	0.082
Animalia	Chordata	Chondrichthyes	Elasmobranchii	Batoidea			23	0.009
Animalia	Chordata						4846	0.609
Animalia	**Cnidaria**	**Anthozoa**	**Actiniaria**				**65**	**0.073**
Animalia	**Cnidaria**	**Hydrozoa**	**Anthoatecata**				**12**	**0.018**
Animalia	**Cnidaria**	**Hydrozoa**	**Leptothecata**	**Lovenellidae**	**Eucheilota**	**maculata**	**11**	**0.018**
Animalia	**Cnidaria**	**Hydrozoa**	**Leptothecata**				**68**	**0.036**
Animalia	**Cnidaria**	**Scyphozoa**					**33**	**0.109**
Animalia	**Ctenophora**	**Tentaculata**					**22**	**0.055**
Animalia	**Mollusca**	**Bivalvia**	**Cardiida**	**Cardiidae**	**Cerastoderma**	**edule**	**6**	**0.036**
Animalia	**Mollusca**	**Bivalvia**	**Myoida**	**Myidae**	**Mya**		**284**	**0.300**
Animalia	**Mollusca**	**Bivalvia**	**Mytiloidea**	**Mytilidae**	**Mytilus**		**386**	**0.427**
Animalia	**Mollusca**	**Bivalvia**	**Ostreida**	**Ostreidae**	**Magallana**	**angulata**	**8**	**0.055**
Animalia	**Mollusca**	**Bivalvia**	**Venerida**	**Veneridae**	**Petricolaria**	**pholadiformis**	**20**	**0.027**
Animalia	**Mollusca**	**Bivalvia**		**Pharidae**	**Ensis**		**17361**	**0.473**

Table S4. Continued.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Total reads	FOO
Animalia	Mollusca	Bivalvia		Pharidae			31	0.036
Animalia	Mollusca	Bivalvia					296	0.282
Animalia	**Mollusca**	**Gastropoda**	**Littorinimorpha**	**Hybrobiidae**	**Peringia**	**ulvae**	**4791**	**0.436**
Animalia	Mollusca	Gastropoda					4304	0.418
Animalia	**Mollusca**	**Polyplacophora**	**Chitonida**	**Mopalioidea**	**Lepidochitonidae**	**cinerea**	**76**	**0.073**
Animalia	Nematoda	Chromadorea	Araeolaimida	Axonolaimidae	Ascolaimus	elongatus	13	0.045
Animalia	Nematoda	Chromadorea	Araeolaimida				80	0.082
Animalia	Nematoda	Chromadorea	Chromadorida	Chromadoridae	Innocuonema	tentabunda	57809	0.836
Animalia	Nematoda	Chromadorea	Chromadorida	Chromadoridae	Punctodora	ratzeburgensis	27253	0.291
Animalia	Nematoda	Chromadorea	Chromadorida				16962	0.600
Animalia	Nematoda	Chromadorea	Desmodoria	Desmodoridae	Desmodora	communis	2222	0.482
Animalia	Nematoda	Chromadorea	Desmodoria	Desmodoridae	Spirinia	parasitifera	28	0.018
Animalia	Nematoda	Chromadorea	Desmodoria	Microlaimidae	Microlaimus	parahonestus	606	0.127
Animalia	Nematoda	Chromadorea	Desmodoria				10620	0.582
Animalia	Nematoda	Chromadorea	Monhysterida	Xyalidae	Daptonema	normandicum	52	0.018
Animalia	Nematoda	Chromadorea	Monhysterida	Xyalidae	Theristus	acer	94	0.064
Animalia	Nematoda	Chromadorea	Monhysterida				3470	0.427
Animalia	Nematoda	Chromadorea	Rhabditida	Spiruridae			85	0.027
Animalia	Nematoda	Chromadorea	Rhabditida	Steinernematidae	Steinernema	kushidai	19	0.009
Animalia	Nematoda	Enoplea	Enoplida	Thoracostomopsidae	Enoploides		382	0.091
Animalia	Nematoda	Enoplea	Enoplida	Thoracostomopsidae			15597	0.309
Animalia	Nematoda	Enoplea	Enoplida	Tripyloididae	Bathylaimus		5	0.009
Animalia	Nematoda	Enoplea	Enoplida	Tripyloididae	Tripyloides		21	0.055
Animalia	Nematoda	Enoplea	Enoplida				28937	0.764
Animalia	Nemertea	Enopla	Monostilifera	Tetrastemmatidae	Tetrastemma	melanocephalum	409	0.082
Animalia	Nemertea	Enopla	Monostilifera				14	0.027
Animalia	Platyhelminthes	Cestoda	Cyclophyllidea				1206	0.173
Animalia	Platyhelminthes	Cestoda					2	0.009
Animalia	Platyhelminthes	Proseriata	Monocelididae				13	0.018
Animalia	Platyhelminthes	Rhabditophora	Dolichomicrostomida	Dolichomacrostomidae	Paromalostomum	dubium	66	0.027
Animalia	Platyhelminthes	Rhabditophora	Rhabdocoela	Dalyellioida			500	0.182
Animalia	Platyhelminthes	Rhabditophora	Rhabdocoela	Kalyptorhynchia			1842	0.182
Animalia	Platyhelminthes	Rhabditophora	Rhabdocoela	Neodalyelllida			690	0.136
Animalia	Platyhelminthes	Trematoda	Plagiorchiida	Microphallidae			5793	0.564
Animalia	Platyhelminthes	Trematoda	Plagiorchiida	Opisthorchiidae			4	0.009
Animalia	Platyhelminthes	Trematoda	Plagiorchiida				23597	0.827

Table S4. Continued.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Total reads	FOO
Animalia	Platyhelminthes	Trematoda					693	0.373
Animalia	Rotifera	Eurotatoria	Ploima	Lindiidae	Lindia	tecusa	60	0.036
Animalia	Rotifera	Eurotatoria	Ploima				312	0.091
Animalia	Tardigrada	Heterotardigrada	Echiniscoidea	Oreellidae	Oreella	mollis	1113	0.336
Animalia	Tardigrada	Heterotardigrada	Echiniscoidea				6	0.027
Animalia	Xenacoelomorpha	Acoela	Isodiametridae	Archaphanostoma	macrospiriferum		74	0.073
Animalia							2720	0.755
Archaeplastida	Charophyta						33168	0.973
Archaeplastida	Chlorophyta						263271	1.000
Archaeplastida	Picozoa						8	0.018
Archaeplastida	Rhodophyta						299	0.273
							509	0.500
Chromista	Cryptophyta						3727	0.636
Chromista	Haptophyta						226	0.255
Chromista	Heliozoa						44	0.109
Eukaryota							88801	1.000
Fungi	Aphelida						17	0.036
Fungi							475562	1.000
Protozoa	Amoebozoa						6452	0.882
Protozoa	Choanozoa						7754	0.927
Protozoa	Excavata						118	0.064
Protozoa	Sulcozoa						2189	0.718
SAR	Alveolata						781588	1.000
SAR	Rhizaria						156375	1.000
SAR	Stramenopiles						370216	1.000
SAR							5471	0.964

Table S5. Results of the simper analysis by the months that were compared. 'average' gives the average contribution of a species to the overall dissimilarity; SD is the standard deviation of the contribution. 'ratio' gives the ratio between average and SD. 'ava' and 'avb' give the average abundance of each month in the comparison. 'cumsum' indicates the cumulative contribution of each species (%) to the dissimilarity between two months.

Contrast: October–July

species	average	SD	ratio	ava	avb	cumsum
Carcinus maenas	0.0859	0.046	1.8519	0.1108	0.3978	0.1590
Crangon crangon	0.0778	0.088	0.8842	0.8040	0.6225	0.3030
Ensis leei	0.0665	0.061	1.0972	0.2871	0.0480	0.4261
Glyceridae	0.0474	0.096	0.4929	0.0000	0.1649	0.5137
Bathyporeia sp.	0.0408	0.039	1.0443	0.1676	0.0634	0.5892
Peringia ulvae	0.0370	0.044	0.8424	0.0080	0.1483	0.6577
Mya arenaria	0.0309	0.061	0.5063	0.0033	0.1058	0.7148
Lanice conchilega	0.0271	0.022	1.2436	0.1377	0.0931	0.7648
Arenicola marina	0.0244	0.019	1.3041	0.1387	0.0788	0.8099
Scoloplos armiger	0.0208	0.020	1.0291	0.0836	0.0568	0.8484
Hediste diversicolor	0.0182	0.020	0.9049	0.0131	0.0684	0.8820
Eteone longa	0.0122	0.011	1.1310	0.0426	0.0287	0.9045
Mytilus edulis	0.0097	0.010	0.9663	0.0387	0.0064	0.9225
Diptera	0.0052	0.011	0.4925	0.0215	0.0000	0.9322
Marenzelleria viridis	0.0051	0.007	0.7179	0.0194	0.0000	0.9416
Actiniaria	0.0048	0.008	0.5768	0.0057	0.0158	0.9504
Gammarus sp.	0.0042	0.007	0.5624	0.0027	0.0158	0.9581
Heteromastus filiformis	0.0038	0.008	0.4786	0.0146	0.0000	0.9651
Corophium sp.	0.0034	0.005	0.6754	0.0129	0.0000	0.9713
Trombidiformes	0.0031	0.010	0.2980	0.0122	0.0000	0.9770
Malacoceros fuliginosus	0.0030	0.006	0.4938	0.0000	0.0126	0.9826
Lepidochitonidae cinerea	0.0028	0.009	0.2980	0.0113	0.0000	0.9879
Collembola	0.0012	0.003	0.4127	0.0048	0.0000	0.9901
Scyphozoa	0.0009	0.003	0.2982	0.0039	0.0000	0.9918
Eucheilota maculata	0.0008	0.003	0.2979	0.0031	0.0000	0.9933
Alitta virens	0.0007	0.002	0.2982	0.0031	0.0000	0.9946
Phyllodoce sp.	0.0007	0.002	0.2981	0.0028	0.0000	0.9958
Tentaculata	0.0007	0.002	0.2981	0.0028	0.0000	0.9971
Anthoatecata	0.0006	0.002	0.2982	0.0027	0.0000	0.9982
Lagis koreni	0.0004	0.001	0.2982	0.0018	0.0000	0.9990
Spionida	0.0003	0.001	0.2979	0.0010	0.0000	0.9995
Capitella sp.	0.0003	0.001	0.2979	0.0010	0.0000	1.0000
Nephtys	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Alitta succinea	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Bylgides sp.	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Spio sp.	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Sessilia	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Coleoptera	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Hymenoptera	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Siphonaptera	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Melita sp.	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Gastrosaccus spinifer	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Praunus flexuosus	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Leptothecata	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Cerastoderma edule	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Magallana angulata	0.0000	0.000	NaN	0.0000	0.0000	1.0000
Petricolaria pholadiformis	0.0000	0.000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5405**					

Table S5. Continued.

Contrast: October–August

species	average	SD	ratio	ava	avb	cumsum
Ensis leei	0.0672	0.0620	1.0828	0.2871	0.0205	0.1291
Crangon crangon	0.0599	0.0506	1.1836	0.8040	0.7082	0.2444
Carcinus maenas	0.0552	0.0515	1.0710	0.1108	0.2660	0.3505
Bathyporeia sp.	0.0401	0.0425	0.9450	0.1676	0.0153	0.4276
Scoloplos armiger	0.0338	0.0442	0.7637	0.0836	0.1202	0.4926
Lanice conchilega	0.0306	0.0248	1.2344	0.1377	0.1144	0.5514
Arenicola marina	0.0298	0.0218	1.3641	0.1387	0.0673	0.6087
Hediste diversicolor	0.0270	0.0411	0.6560	0.0131	0.1112	0.6605
Peringia ulvae	0.0237	0.0508	0.4669	0.0080	0.0986	0.7061
Corophium sp.	0.0207	0.0446	0.4647	0.0129	0.0804	0.7460
Collembola	0.0203	0.0295	0.6865	0.0048	0.0904	0.7849
Diptera	0.0128	0.0220	0.5811	0.0215	0.0405	0.8095
Heteromastus filiformis	0.0128	0.0136	0.9410	0.0146	0.0521	0.8341
Eteone longa	0.0118	0.0107	1.0999	0.0426	0.0254	0.8567
Capitella sp.	0.0114	0.0231	0.4914	0.0010	0.0487	0.8785
Mytilus edulis	0.0113	0.0112	1.0100	0.0387	0.0241	0.9003
Gammarus sp.	0.0081	0.0294	0.2756	0.0027	0.0327	0.9159
Trombidiformes	0.0074	0.0168	0.4399	0.0122	0.0200	0.9301
Marenzelleria viridis	0.0051	0.0068	0.7491	0.0194	0.0020	0.9399
Mya arenaria	0.0051	0.0092	0.5503	0.0033	0.0195	0.9497
Lepidochitonidae cinerea	0.0038	0.0096	0.3926	0.0113	0.0055	0.9569
Actiniaria	0.0028	0.0074	0.3793	0.0057	0.0067	0.9623
Tentaculata	0.0021	0.0080	0.2560	0.0028	0.0063	0.9663
Scyphozoa	0.0018	0.0042	0.4370	0.0039	0.0046	0.9698
Spionida	0.0018	0.0049	0.3678	0.0010	0.0069	0.9733
Glyceridae	0.0016	0.0044	0.3541	0.0000	0.0063	0.9763
Hymenoptera	0.0014	0.0078	0.1760	0.0000	0.0060	0.9789
Phyllodoce sp.	0.0014	0.0038	0.3554	0.0028	0.0032	0.9815
Coleoptera	0.0012	0.0059	0.2071	0.0000	0.0050	0.9839
Anthoatecata	0.0008	0.0026	0.3174	0.0027	0.0010	0.9855
Eucheilota maculata	0.0008	0.0027	0.2989	0.0031	0.0000	0.9871
Petricolaria pholadiformis	0.0007	0.0031	0.2405	0.0000	0.0032	0.9885
Malacoceros fuliginosus	0.0007	0.0030	0.2258	0.0000	0.0028	0.9898
Alitta virens	0.0007	0.0023	0.2995	0.0031	0.0000	0.9911
Alitta succinea	0.0006	0.0045	0.1368	0.0000	0.0025	0.9923
Bylgides sp.	0.0006	0.0033	0.1728	0.0000	0.0024	0.9934
Magallana angulata	0.0006	0.0026	0.2169	0.0000	0.0022	0.9945
Lagis koreni	0.0004	0.0014	0.3256	0.0018	0.0002	0.9954
Praunus flexuosus	0.0004	0.0022	0.1891	0.0000	0.0015	0.9962
Siphonaptera	0.0004	0.0029	0.1369	0.0000	0.0020	0.9969
Gastrosaccus spinifer	0.0004	0.0027	0.1366	0.0000	0.0013	0.9976
Spio sp.	0.0004	0.0023	0.1552	0.0000	0.0013	0.9983
Cerastoderma edule	0.0003	0.0014	0.1839	0.0000	0.0011	0.9988
Sessilia	0.0003	0.0018	0.1366	0.0000	0.0009	0.9993
Nephtys	0.0002	0.0014	0.1829	0.0000	0.0009	0.9998
Leptothecata	0.0001	0.0007	0.1876	0.0000	0.0004	1.0000
Melita sp.	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5201**					

Table S5. Continued.

Contrast: October–September

species	average	SD	ratio	ava	avb	cumsum
Crangon crangon	0.0786	0.0779	1.0087	0.8040	0.6406	0.1437
Ensis leei	0.0674	0.0623	1.0827	0.2871	0.0189	0.2671
Scoloplos armiger	0.0593	0.0577	1.0268	0.0836	0.2694	0.3755
Carcinus maenas	0.0480	0.0633	0.7583	0.1108	0.2208	0.4634
Hediste diversicolor	0.0480	0.0709	0.6765	0.0131	0.1963	0.5511
Bathyporeia sp.	0.0403	0.0406	0.9921	0.1676	0.0356	0.6249
Arenicola marina	0.0275	0.0192	1.4307	0.1387	0.0634	0.6752
Lanice conchilega	0.0262	0.0221	1.1843	0.1377	0.0805	0.7232
Gammarus sp.	0.0245	0.0656	0.3743	0.0027	0.0944	0.7681
Collembola	0.0155	0.0138	1.1234	0.0048	0.0665	0.7965
Eteone longa	0.0128	0.0154	0.8308	0.0426	0.0236	0.8199
Mytilus edulis	0.0118	0.0099	1.1934	0.0387	0.0428	0.8415
Peringia ulvae	0.0099	0.0125	0.7929	0.0080	0.0388	0.8595
Heteromastus filiformis	0.0087	0.0092	0.9422	0.0146	0.0311	0.8755
Corophium sp.	0.0080	0.0134	0.5935	0.0129	0.0261	0.8901
Spio sp.	0.0062	0.0123	0.5065	0.0000	0.0266	0.9015
Diptera	0.0061	0.0102	0.5980	0.0215	0.0072	0.9126
Mya arenaria	0.0055	0.0081	0.6780	0.0033	0.0228	0.9226
Trombidiformes	0.0053	0.0108	0.4859	0.0122	0.0101	0.9322
Glyceridae	0.0050	0.0107	0.4698	0.0000	0.0207	0.9414
Marenzelleria viridis	0.0050	0.0069	0.7187	0.0194	0.0000	0.9506
Capitella sp.	0.0044	0.0090	0.4890	0.0010	0.0170	0.9586
Leptothecata	0.0036	0.0156	0.2323	0.0000	0.0164	0.9653
Lepidochitonidae cinerea	0.0034	0.0097	0.3518	0.0113	0.0032	0.9715
Scyphozoa	0.0028	0.0059	0.4725	0.0039	0.0094	0.9766
Actiniaria	0.0023	0.0056	0.4008	0.0057	0.0038	0.9807
Magallana angulata	0.0016	0.0047	0.3334	0.0000	0.0076	0.9836
Tentaculata	0.0012	0.0036	0.3379	0.0028	0.0026	0.9858
Cerastoderma edule	0.0011	0.0041	0.2572	0.0000	0.0051	0.9878
Sessilia	0.0010	0.0053	0.1951	0.0000	0.0041	0.9897
Eucheilota maculata	0.0010	0.0029	0.3537	0.0031	0.0010	0.9915
Alitta virens	0.0007	0.0023	0.2993	0.0031	0.0000	0.9928
Phyllodoce sp.	0.0007	0.0022	0.2990	0.0028	0.0000	0.9940
Melita sp.	0.0006	0.0032	0.1951	0.0000	0.0025	0.9951
Anthoatecata	0.0006	0.0020	0.2993	0.0027	0.0000	0.9963
Bylgides sp.	0.0005	0.0024	0.1949	0.0000	0.0017	0.9971
Lagis koreni	0.0004	0.0014	0.2993	0.0018	0.0000	0.9979
Alitta succinea	0.0004	0.0019	0.1950	0.0000	0.0014	0.9985
Malacoceros fuliginosus	0.0003	0.0010	0.2719	0.0000	0.0010	0.9991
Spionida	0.0003	0.0009	0.2986	0.0010	0.0000	0.9996
Siphonaptera	0.0002	0.0012	0.1950	0.0000	0.0009	1.0000
Nephtys	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Coleoptera	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Hymenoptera	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Gastrosaccus spinifer	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Praunus flexuosus	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Petricolaria pholadiformis	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5466**					

Table S5. Continued.

Contrast: July–August

species	average	SD	ratio	ava	avb	cumsum
Crangon crangon	0.0807	0.0807	0.9994	0.6225	0.7082	0.1471
Carcinus maenas	0.0750	0.0478	1.5681	0.3978	0.2660	0.2840
Peringia ulvae	0.0479	0.0527	0.9089	0.1483	0.0986	0.3714
Glyceridae	0.0477	0.0936	0.5096	0.1649	0.0063	0.4584
Mya arenaria	0.0327	0.0579	0.5638	0.1058	0.0195	0.5180
Hediste diversicolor	0.0306	0.0376	0.8117	0.0684	0.1112	0.5737
Scoloplos armiger	0.0302	0.0433	0.6977	0.0568	0.1202	0.6288
Lanice conchilega	0.0257	0.0207	1.2379	0.0931	0.1144	0.6756
Collembola	0.0206	0.0302	0.6816	0.0000	0.0904	0.7131
Arenicola marina	0.0205	0.0199	1.0284	0.0788	0.0673	0.7505
Corophium sp.	0.0202	0.0463	0.4369	0.0000	0.0804	0.7874
Bathyporeia sp.	0.0155	0.0173	0.8952	0.0634	0.0153	0.8157
Ensis leei	0.0131	0.0149	0.8781	0.0480	0.0205	0.8395
Heteromastus filiformis	0.0122	0.0146	0.8406	0.0000	0.0521	0.8619
Capitella sp.	0.0113	0.0234	0.4844	0.0000	0.0487	0.8826
Gammarus sp.	0.0103	0.0294	0.3521	0.0158	0.0327	0.9014
Diptera	0.0100	0.0227	0.4410	0.0000	0.0405	0.9197
Eteone longa	0.0100	0.0111	0.9013	0.0287	0.0254	0.9379
Mytilus edulis	0.0062	0.0103	0.6023	0.0064	0.0241	0.9493
Trombidiformes	0.0050	0.0153	0.3267	0.0000	0.0200	0.9584
Actiniaria	0.0048	0.0088	0.5486	0.0158	0.0067	0.9672
Malacoceros fuliginosus	0.0035	0.0063	0.5488	0.0126	0.0028	0.9735
Spionida	0.0016	0.0050	0.3197	0.0000	0.0069	0.9764
Tentaculata	0.0015	0.0080	0.1842	0.0000	0.0063	0.9791
Hymenoptera	0.0014	0.0079	0.1759	0.0000	0.0060	0.9816
Coleoptera	0.0012	0.0060	0.2070	0.0000	0.0050	0.9839
Lepidochitonidae cinerea	0.0012	0.0041	0.2905	0.0000	0.0055	0.9860
Scyphozoa	0.0011	0.0035	0.3140	0.0000	0.0046	0.9881
Phyllodoce sp.	0.0008	0.0034	0.2258	0.0000	0.0032	0.9895
Petricolaria pholadiformis	0.0008	0.0031	0.2404	0.0000	0.0032	0.9909
Alitta succinea	0.0006	0.0045	0.1367	0.0000	0.0025	0.9920
Bylgides sp.	0.0006	0.0034	0.1727	0.0000	0.0024	0.9930
Magallana angulata	0.0006	0.0026	0.2168	0.0000	0.0022	0.9941
Marenzelleria viridis	0.0005	0.0023	0.2253	0.0000	0.0020	0.9950
Praunus flexuosus	0.0004	0.0022	0.1890	0.0000	0.0015	0.9958
Siphonaptera	0.0004	0.0029	0.1368	0.0000	0.0020	0.9965
Gastrosaccus spinifer	0.0004	0.0027	0.1366	0.0000	0.0013	0.9972
Spio sp.	0.0004	0.0023	0.1551	0.0000	0.0013	0.9978
Cerastoderma edule	0.0003	0.0014	0.1839	0.0000	0.0011	0.9983
Anthoatecata	0.0003	0.0019	0.1367	0.0000	0.0010	0.9988
Sessilia	0.0003	0.0018	0.1366	0.0000	0.0009	0.9992
Nephtys	0.0003	0.0014	0.1828	0.0000	0.0009	0.9997
Leptothecata	0.0001	0.0007	0.1876	0.0000	0.0004	0.9999
Lagis koreni	0.0001	0.0004	0.1366	0.0000	0.0002	1.0000
Alitta virens	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Melita sp.	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Eucheilota maculata	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5482**					

Table S5. Continued.

Contrast: July–September

species	average	SD	ratio	ava	avb	cumsum
Crangon crangon	0.0910	0.0858	1.0603	0.6225	0.6406	0.1564
Carcinus maenas	0.0823	0.0519	1.5864	0.3978	0.2208	0.2979
Scoloplos armiger	0.0580	0.0596	0.9727	0.0568	0.2694	0.3975
Glyceridae	0.0499	0.0920	0.5418	0.1649	0.0207	0.4832
Hediste diversicolor	0.0489	0.0654	0.7478	0.0684	0.1963	0.5673
Peringia ulvae	0.0386	0.0384	1.0065	0.1483	0.0388	0.6337
Mya arenaria	0.0331	0.0579	0.5722	0.1058	0.0228	0.6906
Gammarus sp.	0.0262	0.0650	0.4035	0.0158	0.0944	0.7357
Lanice conchilega	0.0196	0.0147	1.3328	0.0931	0.0805	0.7693
Arenicola marina	0.0182	0.0143	1.2693	0.0788	0.0634	0.8006
Bathyporeia sp.	0.0173	0.0178	0.9681	0.0634	0.0356	0.8303
Collembola	0.0162	0.0142	1.1435	0.0000	0.0665	0.8582
Ensis leei	0.0130	0.0150	0.8661	0.0480	0.0189	0.8805
Eteone longa	0.0104	0.0161	0.6483	0.0287	0.0236	0.8984
Mytilus edulis	0.0098	0.0100	0.9796	0.0064	0.0428	0.9153
Heteromastus filiformis	0.0078	0.0093	0.8393	0.0000	0.0311	0.9287
Spio sp.	0.0063	0.0124	0.5057	0.0000	0.0266	0.9395
Corophium sp.	0.0062	0.0146	0.4229	0.0000	0.0261	0.9501
Capitella sp.	0.0043	0.0092	0.4679	0.0000	0.0170	0.9575
Actiniaria	0.0043	0.0076	0.5646	0.0158	0.0038	0.9649
Leptothecata	0.0036	0.0157	0.2320	0.0000	0.0164	0.9712
Malacoceros fuliginosus	0.0032	0.0060	0.5362	0.0126	0.0010	0.9767
Trombidiformes	0.0027	0.0066	0.4077	0.0000	0.0101	0.9813
Scyphozoa	0.0021	0.0057	0.3757	0.0000	0.0094	0.9850
Diptera	0.0017	0.0042	0.4122	0.0000	0.0072	0.9879
Magallana angulata	0.0016	0.0048	0.3328	0.0000	0.0076	0.9906
Cerastoderma edule	0.0011	0.0042	0.2568	0.0000	0.0051	0.9925
Sessilia	0.0010	0.0053	0.1948	0.0000	0.0041	0.9943
Lepidochitonidae cinerea	0.0008	0.0039	0.1948	0.0000	0.0032	0.9956
Melita sp.	0.0006	0.0032	0.1948	0.0000	0.0025	0.9966
Tentaculata	0.0006	0.0031	0.1949	0.0000	0.0026	0.9977
Bylgides sp.	0.0005	0.0024	0.1946	0.0000	0.0017	0.9985
Alitta succinea	0.0004	0.0019	0.1947	0.0000	0.0014	0.9991
Eucheilota maculata	0.0003	0.0013	0.1948	0.0000	0.0010	0.9996
Siphonaptera	0.0002	0.0012	0.1947	0.0000	0.0009	1.0000
Nephtys	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Alitta virens	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Phyllodoce sp.	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Spionida	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Marenzelleria viridis	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Coleoptera	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Hymenoptera	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Gastrosaccus spinifer	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Praunus flexuosus	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Anthoatecata	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Petricolaria pholadiformis	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
Lagis koreni	0.0000	0.0000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5818**					

Table S5. Continued.

Contrast: August–September

species	average	SD	ratio	ava	avb	cumsum
Crangon crangon	0.080320	0.0745	1.0775	0.7082	0.6406	0.1499
Scoloplos armiger	0.062600	0.0611	1.0248	0.1202	0.2694	0.2667
Carcinus maenas	0.060930	0.0636	0.9584	0.2660	0.2208	0.3803
Hediste diversicolor	0.054230	0.0675	0.8030	0.1112	0.1963	0.4815
Gammarus sp.	0.028970	0.0676	0.4282	0.0327	0.0944	0.5356
Peringia ulvae	0.027090	0.0479	0.5651	0.0986	0.0388	0.5861
Lanice conchilega	0.024350	0.0209	1.1654	0.1144	0.0805	0.6315
Collembola	0.023510	0.0253	0.9295	0.0904	0.0665	0.6754
Corophium sp.	0.022780	0.0447	0.5101	0.0804	0.0261	0.7179
Arenicola marina	0.019210	0.0210	0.9143	0.0673	0.0634	0.7537
Capitella sp.	0.013370	0.0223	0.6001	0.0487	0.0170	0.7787
Heteromastus filiformis	0.013320	0.0122	1.0878	0.0521	0.0311	0.8036
Mytilus edulis	0.011490	0.0114	1.0098	0.0241	0.0428	0.8250
Diptera	0.010650	0.0219	0.4870	0.0405	0.0072	0.8449
Bathyporeia sp.	0.010210	0.0138	0.7402	0.0153	0.0356	0.8639
Eteone longa	0.009825	0.0160	0.6148	0.0254	0.0236	0.8822
Mya arenaria	0.007747	0.0101	0.7690	0.0195	0.0228	0.8967
Ensis leei	0.007302	0.0087	0.8386	0.0205	0.0189	0.9103
Trombidiformes	0.006753	0.0151	0.4464	0.0200	0.0101	0.9229
Spio sp.	0.006363	0.0122	0.5223	0.0013	0.0266	0.9348
Glyceridae	0.005860	0.0105	0.5580	0.0063	0.0207	0.9457
Leptothecata	0.003696	0.0154	0.2396	0.0004	0.0164	0.9526
Scyphozoa	0.002943	0.0060	0.4879	0.0046	0.0094	0.9581
Actiniaria	0.002174	0.0064	0.3400	0.0067	0.0038	0.9622
Magallana angulata	0.002019	0.0051	0.3986	0.0022	0.0076	0.9659
Tentaculata	0.002005	0.0083	0.2414	0.0063	0.0026	0.9697
Lepidochitonidae cinerea	0.001848	0.0053	0.3473	0.0055	0.0032	0.9731
Spionida	0.001570	0.0049	0.3191	0.0069	0.0000	0.9760
Hymenoptera	0.001364	0.0078	0.1756	0.0060	0.0000	0.9786
Cerastoderma edule	0.001274	0.0042	0.3024	0.0011	0.0051	0.9810
Sessilia	0.001249	0.0054	0.2293	0.0009	0.0041	0.9833
Coleoptera	0.001218	0.0059	0.2066	0.0050	0.0000	0.9856
Bylgides sp.	0.001011	0.0040	0.2545	0.0024	0.0017	0.9875
Alitta succinea	0.000965	0.0048	0.2019	0.0025	0.0014	0.9893
Malacoceros fuliginosus	0.000934	0.0031	0.3021	0.0028	0.0010	0.9910
Phyllodoce sp.	0.000763	0.0034	0.2253	0.0032	0.0000	0.9924
Petricolaria pholadiformis	0.000742	0.0031	0.2399	0.0032	0.0000	0.9938
Siphonaptera	0.000617	0.0030	0.2035	0.0020	0.0009	0.9950
Melita sp.	0.000614	0.0032	0.1948	0.0000	0.0025	0.9961
Marenzelleria viridis	0.000516	0.0023	0.2248	0.0020	0.0000	0.9971
Praunus flexuosus	0.000411	0.0022	0.1885	0.0015	0.0000	0.9978
Gastrosaccus spinifer	0.000363	0.0027	0.1362	0.0013	0.0000	0.9985
Eucheilota maculata	0.000251	0.0013	0.1948	0.0000	0.0010	0.9990
Anthoatecata	0.000250	0.0018	0.1365	0.0010	0.0000	0.9994
Nephtys	0.000248	0.0014	0.1823	0.0009	0.0000	0.9999
Lagis koreni	0.000050	0.0004	0.1363	0.0002	0.0000	1.0000
Alitta virens	0.000000	0.0000	NaN	0.0000	0.0000	1.0000
overall dissimilarity	**0.5360**					

Table S6. Overview of the taxa that were detected in the negative PCR controls and the negative extraction controls. Lines in bold mark macrobenthic species that were analysed further in our study.

Negative PCR controls

Macrobenthos y/n	Taxon	Total	sampleID			
			P2F0412	P2F0513	P2F0614	P2F0715
n	Calanoida	1	0	1	0	0
y	***Crangon* sp.**	**3**	**0**	**2**	**1**	**0**
n	Podocopida	1	0	0	0	1
n	*Calidris pugnax*	1	0	1	0	0
n	Aves	1	0	0	0	1
n	*Punctodora ratzeburgensis*	3	0	0	3	0
n	Plagiorchiida	1	0	1	0	0
n	Animalia	1	0	0	1	0
n	uncultured fungus	1	0	1	0	0
n	Fungi	1	0	0	0	1
n	Poales	1	1	0	0	0
n	Alveaolata	2	0	0	1	1
n	Fragilariales	1	0	1	0	0
n	Stramenopiles	3	0	0	1	2
n	Eukaryota	5	0	1	0	4
	Total of all reads	26	1	8	7	10

Negative extraction controls

Macrobenthos y/n	Taxon	Total	sampleID		
			P2F0202	P1F1102	P1F1202
n	Charophyta	16,819	0	4902	11,917
n	uncultured fungus	7983	0	4661	3322
n	Fungi	6978	8	195	6775
y	**Collembola***	**5866**	**0**	**7**	**5859**
n	*Prunus persica*	1464	0	3	1461
n	Debaryomycetaceae	1156	0	1	1155
n	Mammalia	446	0	2	444
n	Eimeria	215	0	189	26
n	Dinoflagellata	181	3	79	99
y	***Crangon* sp.***	**93**	**0**	**79**	**14**
n	Ochrophyta	65	0	29	36
n	Opisthokonta	56	0	8	48
n	uncultured Nannochloris	52	0	12	40
n	Eukaryota	40	1	10	29
n	Podocopida	38	0	12	26
n	Enoplida	34	0	10	24
n	*Pycnococcus* sp.	34	0	4	30
n	Prasinoderma	32	2	6	24
n	*Echinostomida* sp.	26	0	0	26
n	uncultured Cercozoa	22	0	4	18
n	*Thoracostomopsidae* sp	17	0	8	9
n	*Thecadinium* sp.	16	0	2	14
n	*Thalassiosira* sp.	15	0	2	13
n	Eugregarinorida	14	0	9	5
n	Phytomyxea	13	0	11	2
n	*Calidris pugnax*	12	1	1	10

Table S6. Continued.

Negative extraction controls

			sampleID		
Macrobenthos y/n	**Taxon**	**Total**	P2F0202	P1F1102	P1F1202
n	Lecudina	10	1	5	4
n	Malassezia	10	0	0	10
n	Metazoa	10	0	0	10
n	*Aspergillus* sp.	8	0	0	8
n	Lankesteria	8	1	2	5
n	Stramenopiles	8	1	3	4
n	Chlorophyta	7	0	0	7
n	*Microphallus primas*	7	0	0	7
n	Stramenopiles	7	0	2	5
n	Alveolata	6	0	4	2
n	Apicomplexa	6	0	0	6
n	Plagiorchiida	6	0	1	5
n	*Prorocentrum cf*	6	1	2	3
n	uncultured Thecofilosea	6	0	1	5
n	Harpacticoida	5	0	2	3
y	***Hediste diversicolor***	**5**	**0**	**0**	**5**
y	***Carcinus maenas***	**4**	**0**	**4**	**0**
n	Cercozoa	4	0	0	4
n	Eimeriorina	4	0	1	3
n	Mediophycea	4	0	2	2
n	Ulvales	4	2	0	2
n	Labyrinthulomycetes	3	0	0	3
n	*Lecudina tuzetae*	3	1	2	0
n	Oligotrichia	3	0	0	3
n	uncultured Apusomonadidae	3	0	0	3
n	uncultured Eukaryote	3	0	0	3
n	uncultured fungus	3	0	3	0
n	uncultured labyrinthulid	3	0	1	2
n	Amoebophrya	2	0	0	2
n	*Amphidinium steinii*	2	0	0	2
n	Amphora	2	0	1	1
n	Bacillariophycea	2	0	2	0
n	*Capsasporidae* sp.	2	0	0	2
n	*Chromadorida* sp.	2	0	0	2
n	*Desmodora communis*	2	1	0	1
n	*Fibrocapsa* sp.	2	0	2	0
n	*Haplosporidium edule*	2	1	0	1
n	Haplotaxida	2	0	0	2
n	*Mychonastes* sp.	2	0	0	2
n	Peronosporomycetes	2	0	0	2
n	*Phagomyxa odontellae*	2	0	0	2
n	Pirsonia	2	0	2	0
n	SAR	2	0	0	2
y	**Teleostei**	**2**	**0**	**0**	**2**
n	*Trichoderma* sp.	2	0	2	0
n	uncultured labyrinthulid	2	0	1	1
n	Amphidinium	1	0	0	1
n	*Amphora coffeiformis*	1	0	0	1
y	***Arenicola marina***	**1**	**0**	**1**	**0**

Table S6. Continued.

Negative extraction controls

Macrobenthos y/n	Taxon	Total	sampleID		
			P2F0202	P1F1102	P1F1202
n	Aves	1	0	0	1
n	*Caenogastropoda* sp.	1	0	1	0
n	Chaetoceros	1	0	1	0
n	*Chromadorita tentabundum*	1	0	0	1
n	Ciliphora	1	0	0	1
y	***Corophium arenarium***	**1**	**1**	**0**	**0**
n	Crustomastix	1	0	0	1
n	*Cucumis sativus*	1	0	1	0
n	*Cymatosira* sp.	1	0	1	0
n	Digenea	1	0	0	1
y	***Ensis directus***	**1**	**0**	**1**	**0**
n	Eucarida	1	0	0	1
n	Eustigmatales	1	0	0	1
y	***Gammarus locusta***	**1**	**0**	**0**	**1**
n	*Harpacticus* sp.	1	0	1	0
y	***Heteromastus filiformis***	**1**	**0**	**1**	**0**
n	*Katablepharis remigera*	1	1	0	0
y	**Lanice conchilega**	**1**	**0**	**0**	**1**
n	*Leptocylindrus* sp.	1	0	0	1
n	*Metschnikowia* sp.	1	0	0	1
n	*Ommatogammarus flavus*	1	1	0	0
n	Paramicrosporidium	1	0	0	1
n	*Paramicrosporidium* sp.	1	0	0	1
y	**Pharidae**	**1**	**0**	**0**	**1**
n	*Prasinoderma singulare*	1	0	0	1
n	Psychodiella	1	0	1	0
n	Rhodomonas	1	0	0	1
n	*Sarocladium* sp.	1	0	0	1
n	*Selenidium terebellae*	1	0	0	1
n	*Semicytherura striata*	1	0	1	0
n	*Solanales* sp.	1	0	0	1
n	Syndiniales Group I	1	0	0	1
n	Trachydiscus	1	0	0	1
n	uncultured alveolate	1	0	0	1
n	uncultured fungus	1	1	0	0
n	uncultured fungus	1	0	0	1
n	uncultured labyrinthulid	1	1	0	0
n	uncultured marine picoeukaryote	1	0	0	1
n	uncultured plasmodiophorid	1	0	1	0
n	uncultured Rhizaria	1	0	0	1
	Total of all reads	41,922	29	10,302	31,591

*Reads in Table S4 were corrected based on these groups