Sand grains in the stomach of brown shrimp, *Crangon crangon*: crunchy garnish, supportive macerator, or simply dirt?

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Abstract

Brown shrimp, *Crangon crangon*, inhabit highly productive sandy and muddy grounds of the southern North Sea. The stomachs of the shrimp contain variable and often high numbers of sediment grains. The function of sediment grains inside the stomach and the purpose of their ingestion are only poorly understood. We tested in laboratory experiments whether sediment and associated organic material complement the natural food of *C. crangon* or if sand grains may be used by the shrimp to support trituration and maceration of ingested food. The shrimp showed no notable preference for sediment with natural organic content over sediment with reduced organic content, limited ingestion of sediment upon starvation, and no additional uptake of sand grains after feeding. Instead, *C. crangon* took up sediment only while feeding on regular food, suggesting that sand grains are not ingested intentionally but rather incidentally as a side effect of hasty gobbling. This conclusion is supported by the highly variable uptake of sand grains among individuals. Under experimental conditions, sand grains from sediments do not seem to have a crucial function in food processing and digestion in brown shrimp.

Key words: Crustacea, North Sea, habitat choice, nutrition, egestion, regurgitation.

1. INTRODUCTION

The brown shrimp *Crangon crangon* (Linnaeus, 1758) is an epibenthic decapod crustacean in the Wadden Sea and in the wider coastal waters of the North Sea (del Norte-Campos & Temming, 1994). *C. crangon* may occur in high numbers of up to 82 individuals per m^2, including juveniles (Boddeke et al., 1986), but population densities show pronounced inter-annual variations (Hünerlage et al., 2019). Ecophysiological adaptations allow *C. crangon* to cope with the variable environmental conditions of the North Sea, including strong fluctuations in temperature, salinity, and food availability (Campos & van der Veer, 2008; Saborowski et al., 2012; Reiser et al. 2014a,b; Martínez-Alarcón et al., 2019).

C. crangon serves as prey for numerous consumers, including fish and larger crustaceans (Redant, 1984; Henderson et al., 1992; del Norte-Campos & Temming, 1998). Additionally, brown shrimp is commercially important, sustaining fisheries in the southern North Sea with a fleet size of 500 vessels (Hünerlage et al., 2019). In 2014, catches of 40,000 tons, worth more than 120 million € were landed in the North Sea, with a German share of 16,000 tons worth 44 million € (STECF, 2016).

As an omnivorous and opportunistic feeder (Wilcox & Jeffries, 1974; Pihl & Rosenberg, 1984; Gibson et al., 1995), *C. crangon* uses a wide spectrum of food organisms. They feed on demersal organisms, such as mysids and juvenile fish (Rauschenplat, 1901; Plagmann, 1939; van der Veer & Bergman, 1987), on epifaunal organisms, such as amphipods and isopods (Ehrenbaum, 1890; Möller & Rosenberg, 1982; Pihl & Rosenberg, 1984), as well as on infaunal species including polycheates and forams (Havinga, 1930; Öhlund et al., 1975; Pihl & Rosenberg, 1984). Occasionally, algae have been found in the stomachs of *C. crangon* (Ehrenbaum, 1890; Plagmann, 1939).

In addition to organic food items, sand grains and mud have regularly been observed in shrimp stomachs (e.g., Ehrenberg, 1890; Plagmann, 1939; Oh et al., 2001). Some studies list sand grains only as a minor food component (Pihl & Rosenberg, 1984) whereas others designate sand and mud as a major constituent of the stomach content of wild shrimp (Plagmann, 1939; Wilcox & Jeffries, 1974; Devriese et al., 2015). Korez et al. (2020) found between 51 and more than 3,000 sand grains within individual stomachs of shrimp from the SE North Sea. Whether sand constitutes an integral part of the diet or is accidentally ingested by the shrimp as a consequence of the natural foraging behavior (Oh et al., 2001) is unknown. Ingested sediment may contribute nutrients derived from the biofilm of associated bacteria and protozoa (Odum, 1971; Wilcox & Jeffries, 1974) or facilitate trituration of the feed (Plagmann, 1939; Tiews, 1970).

In this study, we inspect ingested material inside the stomach and in excretions of *C. crangon* collected in the SE North Sea. In the laboratory, we conducted a habitat choice experiment to evaluate whether *C. crangon* preferentially occupy sediment with natural organic content or cleaned sediment with reduced organic content. Additionally, we performed feeding assays to test if the shrimp take up sand grains intentionally or accidentally while foraging on regular food. Finally, we tested if *C. crangon* ingest sand grains after the uptake of regular food to facilitate maceration of the stomach content.

2. MATERIALS AND METHODS

2.1 Field sampling and maintenance of shrimp

Brown shrimp (*Crangon crangon*) were captured in March and April 2020 in the Weser estuary (53° 42.5´N 8° 17.7´E) by beam trawling (3 m width, 20 mm mesh size in the cod end) in 5 to 11 m depth with the research vessel RV Uthörn. In April, the seawater temperature at the sampling site ranged from 8.1 to 9.8 °C while the salinity varied between 26.0 and 30.6. Hauls lasted for 15 min at a speed of 2 to 3 knots. The shrimp were immediately sorted from the catch and transferred into 40-L flow through aquaria with natural seawater. Additionally, shrimps were immediately isolated from the catch and frozen at -20 °C for the analysis of the stomach content.

Sediment was taken at the same location in 5 m depth with a 0.1 m^2 van Veen grab and transferred into a 10-L bucket for transportation. Shrimp and sediment were shipped to the laboratories of the Alfred Wegener Institute in Bremerhaven. There, the sediment was stored for few days in a cold room at 2 °C until further processing. The shrimp were maintained for about two weeks in flow-through aquaria at a salinity of 34, a constant temperature of 16 °C, and a 12/12 h light/dark cycle. In preparation of the experiments (sections 2.4-2.6), adult individuals were taken randomly from the aquaria and transferred individually into 0.5-L glass jars filled with 400 ml filtered seawater where they were allowed to acclimate for 48 hours to the experimental conditions (temperature: 10 °C, salinity: 32, 12/12 h light/dark). The seawater medium was exchanged after 24 hours.

2.2 Grain size distribution and total organic content of sediment

About 1 kg of the natural sediment from the Weser estuary was dried for 3 days at 60 °C and weighed (± 0.01 g; Sartorius CPA2202S). An electric vibratory sieve shaker (Fritsch analysette 03.502) was used to separate 200 g (dry weight) of the sediment into grain size classes of < 2000 µm, < 1000 µm, < 500 µm, < 250 µm, < 125 µm, < 63 µm. After 20 minutes of sieving, each grain size fraction was weighed and its contribution (%) to the total dry weight of the sediment sample was calculated.

The total organic content (TOM) of the sediment was determined as the loss of dry mass upon ignition. Sediment was dried for 3 days at 60 °C. Six sub-samples of 30 g dry weight each were combusted for 5 hours at 500 °C in a muffle furnace. The share of organic material (M_{org}) was calculated as:

$$M_{org}(\%) = 100\left(\frac{M_{dry} - M_{comb}}{M_{dry}}\right) \qquad \text{Equation 1}$$

with M_{dry} = mass of the oven-dried sediment and M_{comb} = mass of the combusted sediment.

Additionally, treated sediment with reduced organic content was prepared for laboratory experiments. About 5 kg of the sediment was washed three times with demineralised water. Subsequently, the TOM was determined for five sub-samples as described above for the untreated sediment.

The TOM of the five treated and six untreated natural sediment samples were compared by an unpaired t-test after ln-transformation of the data to achieve equal variances (Levene's test: $F_{1,9} = 0.87$, $p = 0.38$). Scanning electron micrographs of the sediment were taken with a FEI Quanta FEG 200 device. The samples were sputter-coated with gold-palladium.

2.3 Analysis of stomach content and excretions

The frozen shrimp were dissected. The stomach was removed and transferred into a 1.5-mL reaction cup. One ml of chlorine solution (DanKlorix, 2.8 g sodium hypochlorite per 100 g liquid) was added to the sample to dissolve the stomach and the organic content. After 2 to 3 hours at room temperature and permanent agitation (Eppendorf, ThermoMix), the stomach fully dissolved and the inorganic remains were collected on a cellulose nitrate filter (Sartorius, 1.2 µm pore size) using a vacuum filtering device and a water jet pump. The filters were dried on air and observed under a stereo microscope (Nikon SMZ25). Scanning electron micrographs of the stomach content were taken.

Additionally, the content of the digestive tract was analysed from material excreted by live individuals, which were isolated immediately upon arrival in the institute and transferred individually into 0.5-L glass jars filled with 400 ml filtered seawater. Ingested material was excreted either along with faecal strings through the hindgut or as regurgitate through the oesophagus. Plaques of regurgitated material on the bottom of the glass jar were inspected under a light microscope. Photos were taken together with a scale and the size of specific items was measured from the images using the software package ImageJ 1.51f (version 1.8.0_77). Scanning electron micrographs of the faecal strings and their contents were taken.

2.4 Experiment 1: Sediment preference

Habitat choice assays were performed to test whether shrimp preferentially occupy natural or cleaned sediment. The jars were aerated through a PVC-tube and the seawater was exchanged daily. During the two days of acclimation, the animals were not fed to induce in the shrimp a behavioural response to a potential nutritional stimulus. After the starvation phase, each animal was transferred individually into a rectangular 5-L aquarium (15 x 25 x 15 cm) filled with seawater (10 °C, salinity 32). One-half of the bottom of the aquarium was layered with two cm of natural sediment and the other half with two cm of cleaned sediment. The aquaria with the shrimp were kept in darkness because shrimp feed primarily in darkness (Wilcox & Jeffries, 1974) and to avoid visual stimuli that may affect the shrimp behaviour. After an acclimation phase of 90 min, the aquaria were visually inspected under dimmed red light to minimize disturbance of the shrimp. The position of the shrimp on natural or cleaned sediment or on the boundary between both sediments was noted every 30 min for 6 h. In total, 12 shrimp were observed. After the experiment, the body length of the shrimp was measured from the tip of the rostrum to the posterior edge of the telson. The shrimp had an average (± SD) body length of 5.5 ± 0.6 cm and a body mass (wet weight) of 5.1 ± 0.6 g. Sex of the shrimp was determined from the presence or absence of an appendix masculinum at the first and second pleopod (Schatte & Saborowski 2006). All specimens used for the experiments were females.

The number of incidences the shrimp were encountered on one of the substratum types (untreated natural sediment, treated sediment) and on the boundary between the sediment types during the 6 h observation period (i.e. 12 measurements per individual) were analysed using a Monte Carlo simulation accounting for the mutual dependency of the choices. The average numbers of incidences for the different substrates were contrasted and the maximum difference between the averages was calculated. Subsequently, the number of choices were randomly shuffled within each replicate and the maximum difference between the averages was determined again. In total, 999 random iteration steps were performed. The probability that a random distribution of substratum choices would result in a higher maximum difference than the observed distribution of choices was estimated as the ratio of maximum differences that were higher than the maximum difference between the real observations. The Monte Carlo simulation was performed using the free software package PopTools (version 3.2).

The boundary zone between the two sediment types was substantially smaller than the areas of the aquarium bottom covered by the two sediment types. Accordingly, a lower probability of encountering the boundary zone may have influenced the choice of the shrimp for this substratum type. Therefore, the mutually dependent choices for the cleaned sediment and the untreated natural sediment (excluding the choices for the boundary zone) were additionally compared by a paired t-test after a D'Agostino and Pearson normality test had confirmed the normal distribution of the differences between the paired choices.

2.5 Experiment 2: Sediment as food source

To investigate whether the uptake of sediment by the shrimp depends on the organic content of the sediment and/or on the presence of food, twelve acclimated shrimp each were transferred individually into 0.5-L glass jars with 400 ml of filtered seawater and subjected to one of the following five treatments:

(1) Control group with no sediment and no food

(2) 2-cm bottom layer of untreated natural sediment and no additional food

(3) 2-cm bottom layer of cleaned sediment and no additional food

(4) 2-cm bottom layer of untreated natural sediment and additional food (300-400 mg of shrimp abdominal muscle)

(5) 2-cm bottom layer of cleaned sediment and additional food (300-400 mg of shrimp abdominal muscle)

After 16 h of exposure, body length and mass of each individual were measured and the animals were frozen at -80 °C. The average body length of the shrimp ranged from 5.3 ± 0.4 cm to 5.5 ± 0.4 cm and did not vary between the treatments (ANOVA: $F_{4,55} = 0.56$; $p = 0.69$).

The average body mass (wet weight) ranged from 1.8 ± 0.4 g to 2.1 ± 0.4 g and did not vary between the treatments (ANOVA: $F_{4,55} = 0.75$; $p = 0.56$).

The stomach content was isolated and dried on filters as described above for the stomach content analysis. Photographs of the ingested sediment grains were taken for subsequent counting. Only sediment grains ≥ 75 µm were considered for this study.

The average numbers of sand grains inside the stomach were compared between the treatments using a one-factorial Analysis of Variance (ANOVA) although the variances were significantly heterogeneous among groups. However, data transformation was not able to achieve homoscedasticity (Levene’s test: $F_{4,55} = 8.78$; $p < 0.01$). Tukey’s HSD test was used for multiple comparison after ANOVA.

2.6 Experiment 3: Sediment ingestion to facilitate food maceration

To test whether shrimp ingest sediment to facilitate food maceration, twelve acclimated shrimp each were individually transferred into new glass jars with filtered seawater and were exposed to one of the following four treatments:

(1) No food. After three hours, the shrimp were transferred into new glass jars with filtered seawater and a 2-cm bottom layer of untreated natural sediment.

(2) No food. After three hours, the shrimp were transferred into new glass jars with filtered seawater and a 2-cm bottom layer of clean sediment.

(3) 300-400 mg of shrimp abdominal muscle offered as food. After three hours, the shrimp were transferred into new glass jars with filtered seawater and a 2-cm bottom layer of untreated natural sediment.

(4) 300-400 mg of shrimp abdominal muscle offered as food. After three hours, the shrimp were transferred into new glass jars with filtered seawater and a 2-cm bottom layer of clean sediment.

After another 3 hours, the experiment was terminated. The biometric data were recorded and the shrimp were frozen for subsequent quantification of sand grains inside the stomach as described above. The average body length of the shrimp ranged from 5.5 ± 0.4 cm to 5.7 ± 0.4 cm and did not vary between the treatments (ANOVA: $F_{3,45} = 0.61$; $p = 0.19$). The average body mass (wet weight) ranged from 2.2 ± 0.5 g to 2.4 ± 0.5 g and did not vary between the treatments (ANOVA: $F_{3,45} = 0.19$; $p = 0.90$). The average numbers of sand grains inside the stomach was compared between treatments by a one-factorial ANOVA.

3. RESULTS

3.1 Grain size distribution and organic content of the sediment

The dominant grain size fractions of the sediment from the Weser estuary were the fraction 63 to ≤ 125 µm and 125 - ≤ 250 µm, which accounted for 58 % and 37 %, respectively, of the total sediment dry mass. The silt and clay fraction (grain size < 63 µm) was small and accounted for only 2 % of the total sediment dry mass. According to the classification by Hiscock (1996), the sediment was categorized as fine sand.

The surface of the natural sand grains showed an irregular and undefined crusty layer with some fragments of diatom shells embedded (Figure 1, Panel A). The surface of the cleaned sediment was smooth without adherent crust. No remains of inorganic or organic materials adhered to the surface of the cleaned sand grains (Figure 1, Panel B).

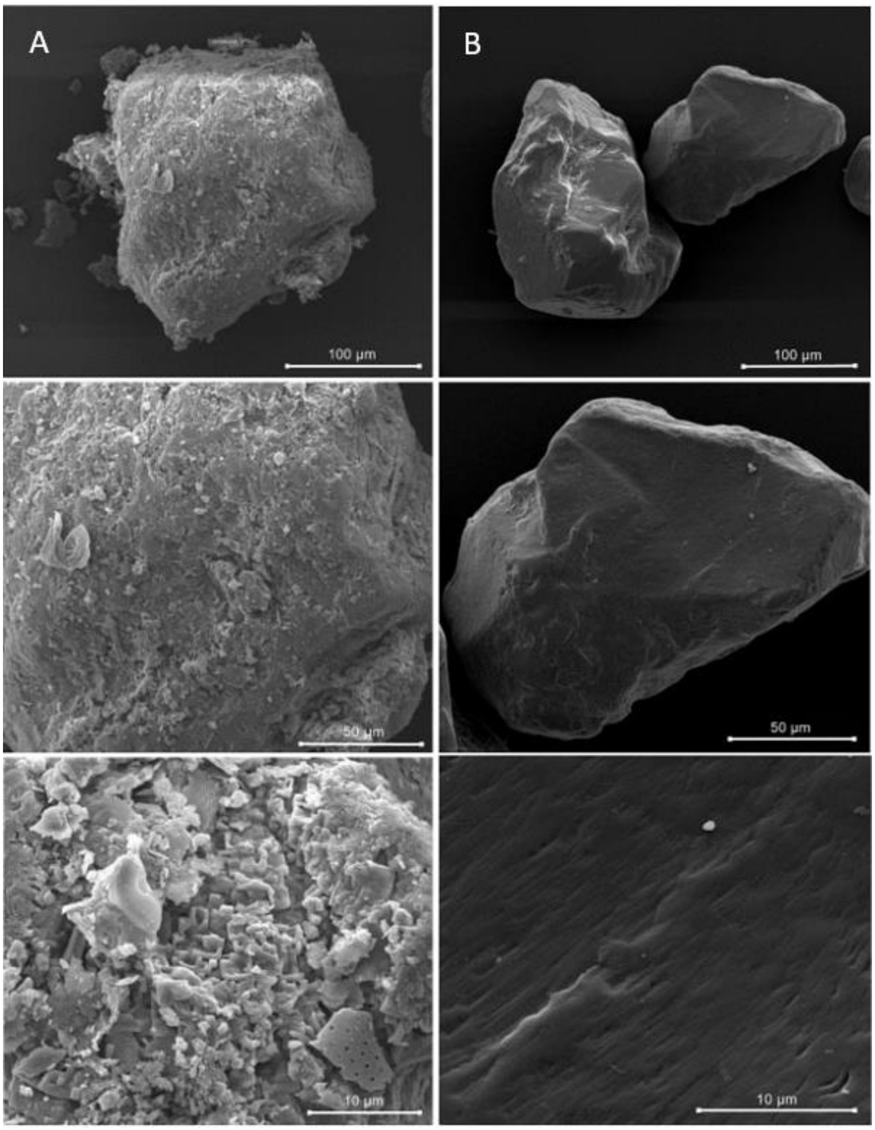

Figure 1. Scanning electron micrograph of A) untreated natural and B) cleaned sediment. The photographs of each panel show from top to bottom series of increasing magnification of the same object.

On average (± SD), the TOM content of the natural sediment accounted for 1.09 ± 0.17 % of the sediment dry mass (Figure 2). Washing and drying reduced the TOM content of the sediment by the factor 4.5 to 0.24 ± 0.03 % of the sediment dry mass. The TOM content differed significantly between untreated natural and cleaned sediment (unpaired t-Test of ln-transformed data: $t_9 = -14.9$; $p < 0.01$).

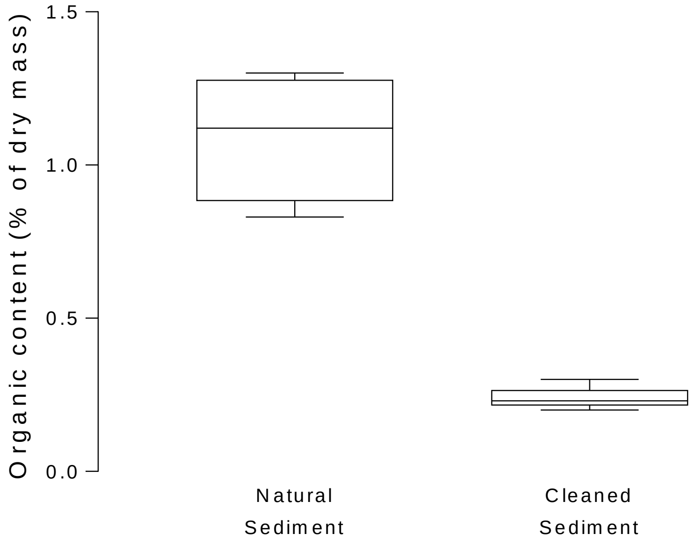

Figure 2. Total organic matter (TOM) content of untreated natural (n = 6) and cleaned sediment (n = 5). The boxes extend from 25th to 75th percentiles with the median as vertical line; whiskers display minimum and maximum values.

3.2 Stomach content

The stomachs contents of *Crangon crangon* contained numerous sand grains embedded in a matrix of undefined mashed material (Figure 3). Similarly, regurgitated stomach content also consisted of sand grains, spines (presumably bristles of polychaetes) and undefined mashed material (Figure 4). Parts of the mashed material showed a fibrous texture while other parts resembled an amorphous layer. The sand grains were of irregular shape. The surface of the sand grains appeared smooth. Their size ranged from about 100 to 300 µm.

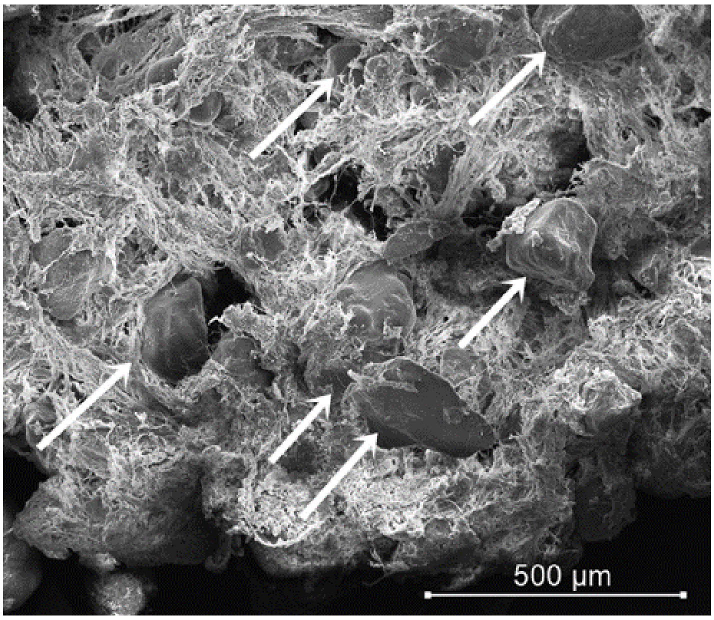

Figure 3. Scanning electron micrograph of stomach content of *Crangon crangon* showing sand grains (arrowheads) within a matrix of mashed organic material.

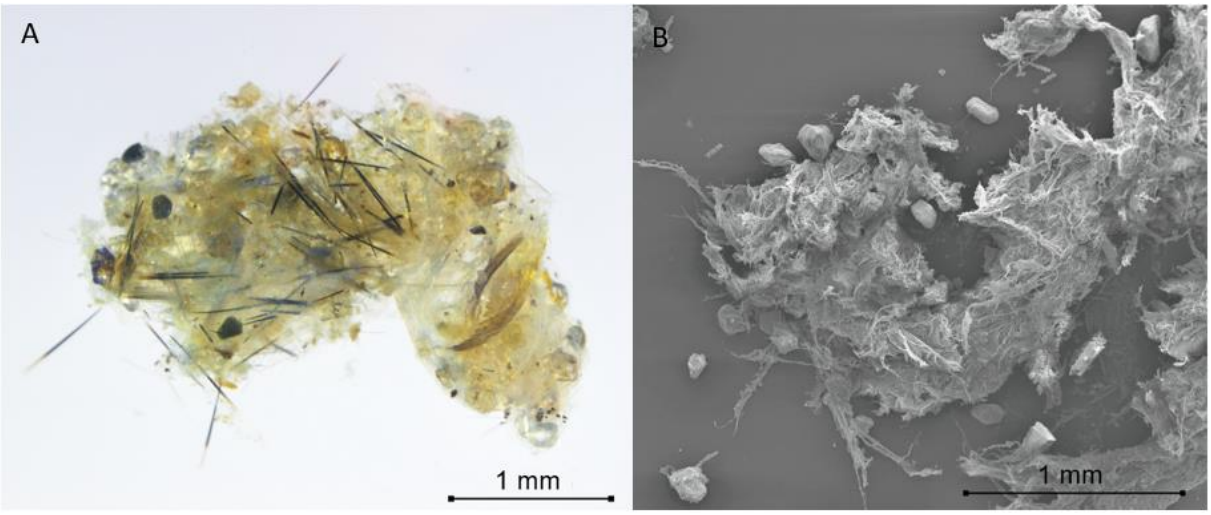

Figure 4. A) Photo and B) scanning electron micrograph of regurgitated stomach content of *Crangon crangon*.

The faecal strings of *C. crangon* (Figure 5a) had diameter from 39 to 205 µm (mean ± SD of 24 measurements: 89 ± 56 µm). They contained small fragments of diatoms and undefined organic material (Figure 5b).

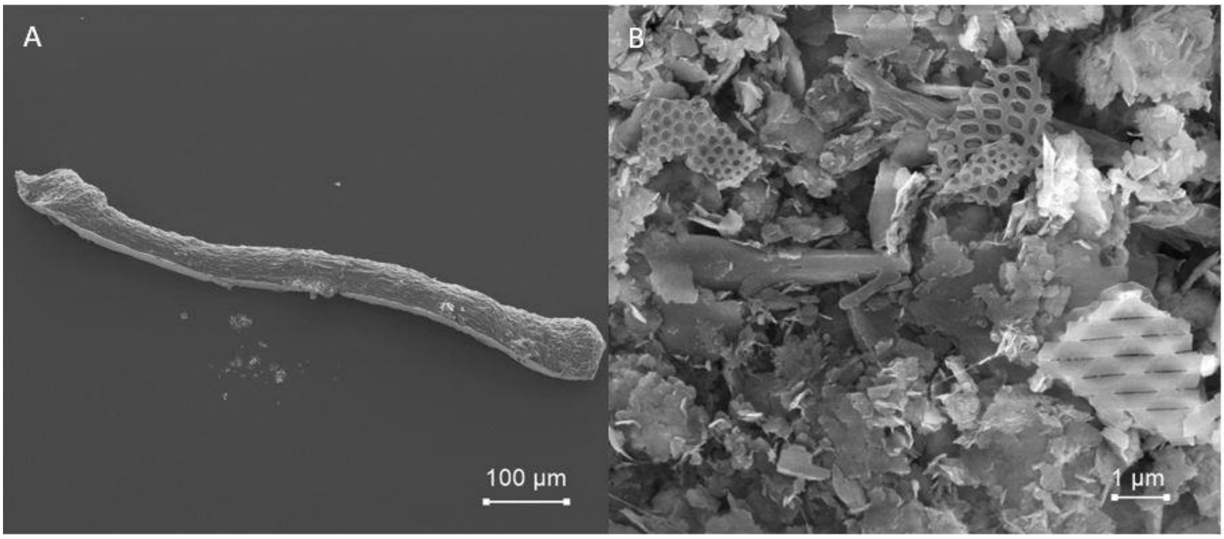

Figure 5. A) Scanning electron micrographs of a faecal string of *Crangon crangon* and B) the content of a faecal string.

3.3 Experiment 1: Sediment preference

Most of the shrimp remained on the sediment, on which they were first observed 90 min after they were placed into the aquaria. Five individuals were observed exclusively on the natural sediment, two shrimp were only on the treated sediment, and one shrimp continuously occupied the boundary between both sediments. Four shrimp switched between the sediment types thereby crossing the boundary between the sediments. During the six hours observation period, the shrimp were on average 6.1 ± 5.0 times on the natural sediment and 3.8 ± 4.4 times on the treated sediment (Figure 6). The shrimp were observed on the boundary between the two sediments only 2.2 ± 3.7 times. The maximum difference in the average number of observations per sediment of 3.9 was exceeded in the Monte Carlo simulation for 210 out of 999 iteration steps. Accordingly, the probability of $p = 0.21$ of observing a difference larger than the observed one from a random distribution of observations suggests that the shrimps did not show a clear substratum preference. Similarly, the comparison of the number of observations between the natural and the treated sediment only did not confirm any preference (paired t-test: $t_{11} = 0.94$; $p = 0.37$).

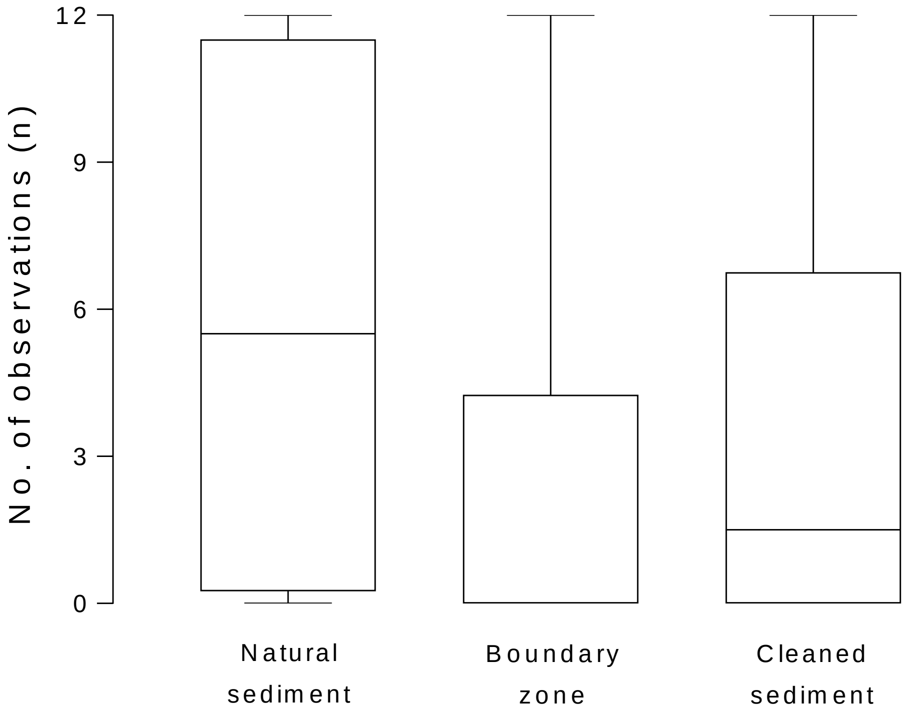

Figure 6. Number of observations of *Crangon crangon* on untreated natural sediment, cleaned sediment and on the boundary between the two sediment types during the six hours observation period (n = 12). The boxes extend from 25th to 75th percentiles with the median as vertical line; whiskers display minimum and maximum values.

3.4 Experiment 2: Sediment as food source

Control shrimp and shrimp that did not receive food contained only few sand grains in their stomachs (Figure 7). On average, the control animals carried 1.0 ± 1.4 sand grains in their stomachs whereas shrimp on natural and cleaned sediment had 8.5 ± 1.7 and 2.8 ± 3.1 sand grains in their stomachs, if they had no access to food. On both sediments, high numbers of sand grains were observed only in shrimp that received food. However, the amount of ingested sand grains varied considerably among individuals. On natural sediment, the shrimp stomachs contained 2 to 352 sand grains (mean: 69.1 ± 105.3) and 0 to 774 sand grains (125.8 ± 238.0) on treated sediment. Despite the high within-group variation the one-factorial ANOVA indicated significant differences between the treatments ($F_{4,55} = 2.68$; $p = 0.04$). However, the extreme heteroscedasticity enhanced the probability of a type 1 error (i.e. erroneously assuming a difference). The Tukey's HSD test did not confirm significant differences in pairwise comparisons.

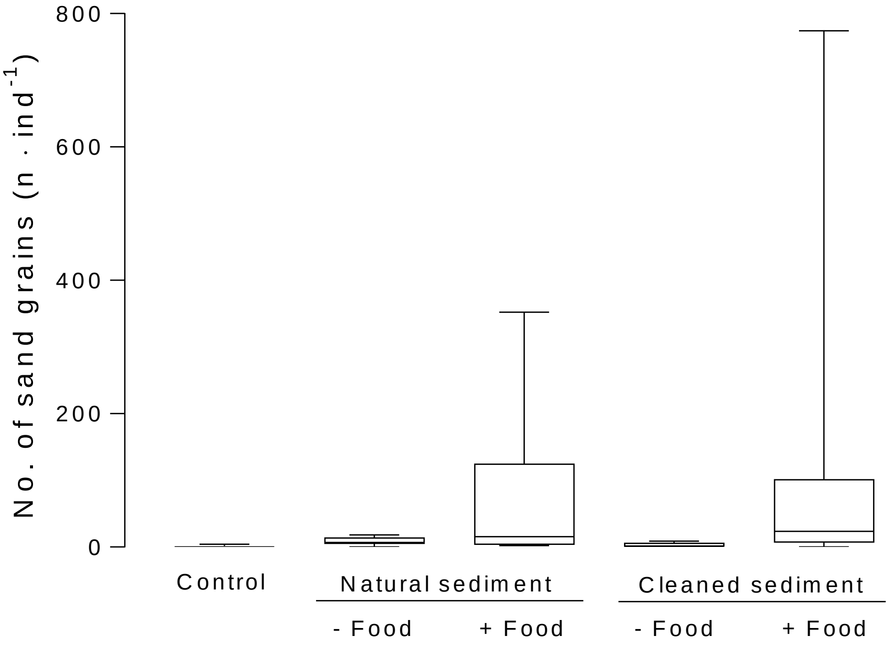

Figure 7. Number of sand grains in stomachs of *Crangon crangon* on untreated natural sediment and cleaned sediment with food and without food (n = 12). The boxes extend from 25th to 75th percentiles with the median as vertical line; whiskers display minimum and maximum values.

3.5 Experiment 3: Sediment ingestion to facilitate food maceration

Shrimp that had access to sand grains after feeding never had high numbers of sand grains in their stomachs (Figure 8). Starved shrimp placed on natural sediment contained a maximum of 9 (mean: 2.1 ± 2.3) sand grains, fed animals a maximum of 30 (mean: 6.3 ± 7.8) sand grains. Shrimp that were placed on clean sediment contained a maximum of 27 (mean: 7.9 ± 8.8) sand grains when starved and a maximum of 12 (mean: 2.7 ± 3.5) sand grains when fed. The differences in the average number of sand grains in the stomachs did not vary between individuals from different treatments (ANOVA: $F_{3,44} = 2.27$; $p = 0.09$).

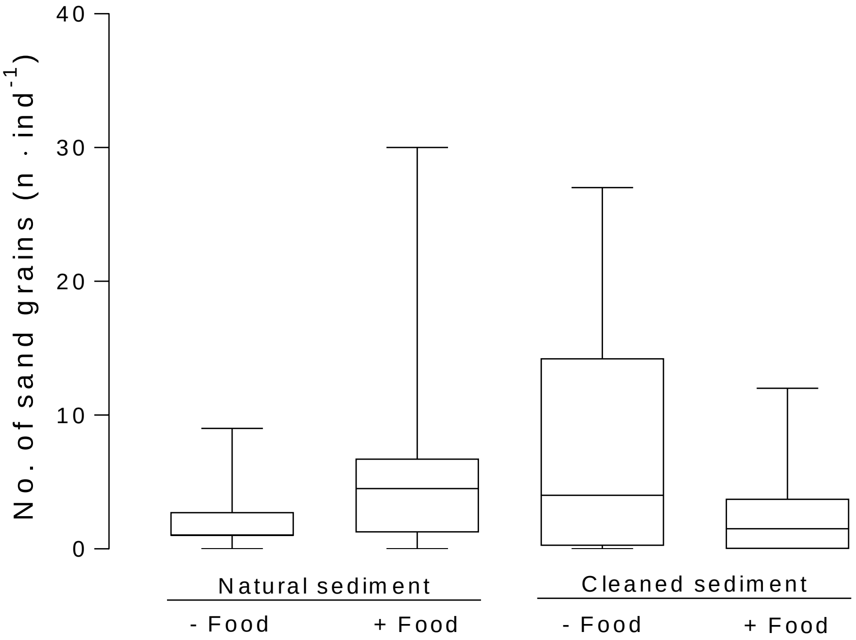

Figure 8. Number of sand grains in the stomachs of starved *Crangon crangon* and in stomachs of individuals that were fed prior to exposure to untreated natural or cleaned sediment (n = 12). The boxes extend from 25th to 75th percentiles with the median as vertical line; whiskers display minimum and maximum values.

4. DISCUSSION

Stomach contents of *Crangon crangon* from the Weser estuary in the SE North Sea contained considerable amounts of sediment clearly demonstrating that the shrimp ingest sand grains in their natural environment. Previous studies hypothesized that ingested sediment may provide nutrients (Odum, 1971; Wilcox & Jeffries, 1974) or facilitate trituration of the food (Plagmann, 1939; Tiews, 1970). However, our laboratory experiments did not confirm a crucial role of sand grains in the diet of *C. crangon*. Instead, sediment may be taken up accidentally by the shrimp during regular foraging.

C. crangon inhabits shallow sandy and muddy grounds (Pinn & Ansell, 1993; Barnes, 1994) in highly productive estuaries with strong tidal water movements (Tiews, 1970). The seafloor of the shallow SE North Sea is characterized by a complex pattern of variable sediments and extensive sandy and muddy intertidal areas of the Wadden Sea (Wang et al., 2012; Bockelmann et al., 2018). Intense pelagic and benthic primary production in the nutrient-rich coastal waters form the base of a considerable organic enrichment of the sediments, especially in the estuaries of major rivers, which contribute organic material from inland primary and secondary production (Eisma & Kalf, 1987).

The organic load of the untreated natural sediment was clearly visible in scanning electron micrographs as an adherent crust with fragments of diatoms and other unidentifiable organic material. The organic crust of the sediment was easily removed by repeated washing in freshwater suggesting that the organic material is only loosely bound to the surface of the sediment grains. Similarly, it may be mechanically extracted by constant friction of ingested sand grains induced by the stomach peristalsis of the shrimp. The use of sediment-bound organic material by benthic consumers has been demonstrated for several species, such as the thalassinid shrimp *Callianassa tyrrhena* and amphipods of the genus *Bathyporeia* (Nicolaisen & Kanneworff, 1969; Dworschak, 1987). Microscopic inspection of the stomach content and regurgitates clearly confirmed the uptake of sand grains by *C. crangon* in their natural environment (see also Korez et al. 2020). Similarly, sand grains or mud were regularly observed in stomachs of brown shrimp in previous studies (Ehrenbaum, 1890; Plagmann, 1939; Oh et al., 2001). The surfaces of the sand grains in the stomach were clean and smooth. However, it remains unclear whether the organic crust was removed from the surface as part of a digestive process or simply through mechanical abrasion within the densely packed stomach content.

Inside the stomach, the sand grains were embedded in a rich amorphous matrix, probably consisting of regular food material. Accordingly, organic material adhering to the sand grains may constitute only a minor fraction of the total food, at least in times when abundant alternative food is available. Previous observations indicate that *C. crangon* may at least temporarily feed on sediment. Ehrenbaum (1890) described the nutritive state of shrimp in spring as poor and mentioned a higher number of unappetising mud containing shrimp with a musty taste. Hufnagl et al. (2010) reported that the majority of the shrimp population is food limited in winter. Accordingly, shrimp may shift their diet seasonally, and may revert to sediment and detritus feeding during periods of severe food limitation.

Food availability can be an important determinant for habitat selection in shrimp. For example, sand shrimp, *Crangon septemspinosa*, prefer sandy sediment over peat substratum. In habitat choice experiments, however, the addition of food to the peat substratum clearly enhanced the preference of the shrimp for the otherwise avoided sediment type (Ouellette et al. 2003). *C. crangon* did not distinguish between untreated natural sediment and cleaned sediment with reduced organic content even though the animals had been starving prior to the experiment for 48 hours. Experimental cleaning reduced the total organic content of the sediment by 78 %.

Still, the reduced organic content of 0.24 % is within the range of sediments in suitable habitats and nursery grounds of *C. crangon* in the SE North Sea. For example, organic contents of 0.2-0.8 % in sand were found in sediments around the island of Sylt in the northern part of the German Wadden Sea (Kristensen et al., 1997). Apparently, the organic material in the sediment is not perceived by the shrimp as a valuable food resource, or the difference in the food availability between the untreated natural sediment and the treated sediment was insufficient to induce a clear habitat choice response in *C. crangon*.

Indigestible inorganic fractions of the food, such as shells and sand grains, affect the overall nutritional value of ingested material (Pihl & Rosenberg, 1984). Similarly, a limited nutritional quality of the sediment was indicated by the results from our feeding experiment. When no additional food was offered, the shrimp ingested only very few sand grains no matter if the sediment was untreated or cleaned. However, when additional food was offered some shrimp ingested considerable amounts of sediment. Similarly, Plagmann (1939) observed that starved shrimps did not ingest sediment if no additional food could be sensed. Sediment grains are often found in the stomachs of *C. crangon* together with algal material (Pihl & Rosenberg, 1984) and animal prey, such as crustaceans (Wilcox & Jeffries, 1974). Sand grains may adhere to the food items or stick to dissected parts of the food while being processed by the mouthparts. Additionally, prey organisms, such as some polychaetes and crustaceans, may contain substantial amounts of sediment grains in their own digestive organs, which finally appear in the stomach of the brown shrimp. Accordingly, the uptake of sediment together with other food items is a stochastic event explaining why some individuals in our experiments had only few sand grains in their stomachs although additional food was offered. A great variability in the sediment load in the stomachs of *C. crangon* was observed also in previous studies. Some shrimp contained only few grains whereas others had stomachs completely filled with sediment (Plagmann, 1939; Pihl & Rosenberg, 1984; Devriese et al., 2015). Depending on the prey species and the sediment structure, the amount of adhering and incorporated sand grains may vary (Ehrenbaum, 1890; Plagmann, 1939). Similarly, the stickiness of chopped tissue such as the muscle tissue in our experiments and its contact to the sediment during feeding likely alters the sediment load of the ingested food.

The irregular but smooth surfaces of the cleaned sand grains suggest that these particles may, upon ingestion, facilitate the grinding of food items inside the stomach of *C. crangon*. Different from many other benthic crustaceans, such as crayfish and crabs, *C. crangon* does not possess an explicit gastric mill. Therefore, it has been suggested, that the uptake of sediment grains facilitates the maceration of ingested food (Plagmann, 1939). However, the efficiency of shredding may be limited at least for certain types of food. For example, nematodes were still alive in the stomach of *C. crangon* for up to 30 min after ingestion and body parts remained intact for 1 to 2 hours after ingestion (Gerlach & Schrage 1969). Similarly, parts of ingested polychaetes were still present in the stomach 6 hours after ingestion (N. Schmidt, pers. obs.), indicating no efficient maceration of the food by ingested sand grains. Similarly, the results of our third experiment do not support the hypothesis that sand grains are ingested by *C. crangon* to promote food maceration because individuals that had been feeding before did not ingest more sand grains than individuals without access to food. Alternatively, the shrimps may selectively take up sand grains to support maceration of poorly digestible food items that require mechanical forcing, such as small bivalves. In our experiment, the shrimp received relatively soft abdominal muscle tissue from conspecifics, which may not require additional mechanical treatment.

Indigestible items, including sediment grains and polychaete bristles, were evacuated from the stomach through the esophagus rather than through the hindgut. Regurgitation of the non-digestible sediment grains by *C. crangon* and other shrimp species was also observed in previous studies (Plagmann, 1939; Pihl & Rosenberg, 1984; Saborowski et al., 2019). The oesophagus of caridean shrimps is a dilatable organ. The lumen diameter is controlled by extrinsic muscles, surrounding the esophagus. The wall is slightly folded which facilitates tight closure but also wide distention (Felgenhauer & Abele, 1985). In our laboratory cultures, medium sized *C. crangon* easily ingested polychaetes with a diameter of about 2 mm (N. Schmidt, pers. obs.). The gut, in contrast, has a more delicate structure and appears more vulnerable against mechanical damage. It is suited to pass small and soft food remains towards the hindgut. Moreover, the undigested material is covered by a peritrophic membrane to protect the gut epithelium (Peters, 1968). It leaves the body as a faecal string with a diameter of about 90 µm. We found small fragments of diatoms and undefined organic material within the faecal strings. Large, sharp, and spiky items may be retained by the pyloric filter and, therefore, not enter the midgut and the hindgut of the shrimp (Korez et al. 2020). Most of the ingested sand grains were larger than 100 µm (Korez et al. 2020, this study). Apparently, the gut of *C. crangon* is too narrow for the large sand grains of up to 400 µm to pass through. Consequently, the faecal material contained no large items but mostly tiny fragments of e.g. diatom frustules together with undefined organic material.

In summary, the uptake of sediment by *C. crangon* seems to be a common event. However, the organic content of the sediment seems to be of minor nutritional importance in comparison with other food items. Similarly, ingested sand grains may not be particularly important for the maceration of ingested food items. Instead, the shrimp likely take up sand grains accidentally while foraging on a great variety of plant and animal prey. Sediment-bound organic material may seasonally become a dietary supplement for *C. crangon* during periods of severe food limitation.

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6. REFERENCES

Barnes RSK (1994) The brackish-water fauna of northwestern Europe. *Cambridge University Press*. Cambridge, 303 pp.

Bockelmann F-D, Puls W, Kleeberg U, Müller D, Emeis K-C (2018) Mapping mud content and median grain-size of North Sea sediments – a geostatistical approach. *Marine Geology* 397, 60-71. https://doi.org/10.1016/j.margeo.2017.11.003

Boddeke R, Driessen G, Doesburg W, Ramaekers G (1986) Food availability and predator presence in a coastal nursery area of the Brown Shrimp (*Crangon crangon*). *Ophelia* 26, 77-90. https://doi.org/10.1080/00785326.1986.10421980.

Campos J, van der Veer HW (2008) Autecology of *Crangon crangon* (L.) with an emphasis on latitudinal trends. *Oceanography and Marine Biology: An Annual Review* 46, 65-104. https://doi.org/10.1201/9781420065756.ch3.

del Norte-Campos AGC, Temming A (1994) Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea. *Marine Ecology Progress Series* 115, 41-53. https://doi.org/10.3354/meps115041.

del Norte-Campos AGC, Temming A (1998) Population dynamics of the brown shrimp *Crangon crangon* L., in shallow areas of the German Wadden Sea. *Fisheries Management and Ecology* 5, 303-322. https://doi.org/10.1046/j.1365-2400.1998.540303.x.

Devriese LI, van der Meulen MD, Maes T, Bekaert K, Paul-Pont I, Frère L, Robbens J, Vethaak AD (2015) Microplastic contamination in brown shrimp (*Crangon crangon*, Linnaeus 1758) from coastal waters of the Southern North Sea and Channel area. *Marine Pollution Bulletin* 98, 179–187. https://doi.org/10.1016/j.marpolbul.2015.06.051.

Dworschak PC (1987) Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea). *Investigacion Pesquera* 51, 421-429.

Ehrenbaum E. (1890) Zur Naturgeschichte von *Crangon vulgaris* Fabr., Studien über Bau, Entwicklung, Lebensweise und Fangverhältnisse des Nordsee-Granat. *Sonderbeilage zu den Mitteilungen der Sektion für Küsten-und Hochseefischerei*, pp. 9-124.

Eisma D, Kalf J (1987) Dispersal, concentration and deposition of suspended matter in the North Sea. *Journal of the Geological Society* 144, 161-178. https://doi.org/10.1144/gsjgs.144.1.0161.

Felgenhauer BE, Abele LG (1985) Feeding structures of two atyid shrimps, with comments on caridean phylogeny. *Journal of Crustacean Biology* 5, 397-419. https://doi.org/10.2307/1547911.

Gerlach SA, Schrage M (1969) Free-living nematodes as food of the sand shrimp, *Crangon crangon*: experiments on the role of meiofauna as food of the marine macrobenthos. *Oecologia* 2, 362-375. https://doi.org/10.1007/bf00778992.

Gibson RN, Yin MC, Robb L (1995) The behavioural basis of predator–prey size relationship between shrimp *(Crangon crangon*) and juvenile plaice *(Pleuronectes platessa)*. *Journal of the Marine Biological Association of the United Kingdom* 75, 337–349. https://doi.org/10.1017/S002531540001821X.

Havinga B (1930) Der Granat *(Crangon vulgaris* Fabr.) in den holländischen Gewässern. *ICES Journal of Marine Science* 5, 57–87. https://doi.org/10/1093/icesjms/5.1.57.

Henderson PA, James D, Holmes HA (1992) Trophic structure within the Bristol Channel: seasonality and stability in Bridgwater Bay. *Journal of the Marine Biological Association of the United Kingdom* 72, 675-690. https://doi.org/10/1017/S0025315400059440.

Hiscock K (ed.) (1996) *Marine Nature Conservation Review: rationale and methods*. Peterborough, Joint Nature Conservation Committee. (Coasts and seas of the United Kingdom. MNCR series.)

Hufnagl M, Temming A, Dänhardt A, Perger R (2010) Is *Crangon crangon* (L. 1758, Decapoda, Caridea) food limited in the Wadden Sea? *Journal of Sea Research* 64, 386-400. https://doi.org/10.1016/j.seares.2010.06.001.

Hünerlage K, Siegel V, Saborowski R (2019) Reproduction and recruitment of the brown shrimp, *Crangon crangon* in the inner German Bight (North Sea): an interannual study and critical reappraisal. *Fisheries and Oceanography* 28, 708–722. https://doi.org/10.1111/fog.12453.

Korez Š, Gutow L, Saborowski R (2020) Coping with the “dirt”: brown shrimp and the microplastic threat. Zoology 143, 125848. https://doi.org/10.1016/j.zool.2020.125848

Kristensen E, Jensen MH, Jensen KM (1997) Temporal variations in microbenthic metabolism and inorganic nitrogen fluxes in sandy and muddy sediments of a tidally dominated bay in the northern Wadden Sea. *Helgoländer Meeresuntersuchungen* 51, 295-320. https://doi.org/10.1007/BF02908717.

Martínez-Alarcón D, Harms L, Hagen W, Saborowski R (2019) Transcriptome analysis of the midgut gland of *Crangon crangon* indicates high polymorphism in digestive enzymes. *Marine Genomics* 43, 1-8. https://doi.org/10/1016/j.margen.2018.09.006.

Möller P, Rosenberg R (1982) Production and abundance of the amphipod *Corophium volutator* in some marine habitats on the west coast of Sweden. *Netherlands Journal of Sea Research* 16, 127-140. https://doi.org/10.1016/0077-7579(82)90024-2.

Nicolaisen W, Kanneworff E (1969) On the burrowing and feeding habits of the amphipods *Bathyporeia pilosa Lindström* and *Bathyporeia sarsi Watkin*. *Ophelia* 6, 231-250. https://doi.org/10.1080/00785326.1969.10409651.

Odum WE (1971) Pathways of energy flow in a south Florida estuary. *Sea Grant Technology Bulletin* 7, 1-162.

Öhlund E, Olsson I, Rosenberg R, Thorell L (1975) The By Fjord: ecological investigations on zooplankton, benthic meio- and macrofauna and bacteria in the By Fjord. *Swedish Environmental Protection Board P. M.* 568, 1-94.

Oh C-W, Hartnoll RG, Nash RDM (2001) Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. *Marine Ecology Progress Series* 214, 211-223. https://doi.org/10. 3354/meps214211.

Ouellette C, Bighen AD, Courtenay SC, St-Hilaire A (2003) Influence of peat substrate on the distribution and behaviour patterns of sand shrimp, *Crangon septemspinosa*, under experimental conditions. *Journal of Applied Ichthyology* 19, 359-365. https://doi.org/10.1046/j.0175-8659.2003.00498.x.

Peters W (1968) Vorkommen, Zusammensetzung und Feinstruktur peritrophischer Membranen im Tierreich. *Zeitschrift für Morphologie der Tiere* 62, 9-57. https://doi.org/10.1007/BF00401488.

Pihl L, Rosenberg R (1984) Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Marine Ecology Progress Series* 15, 159–168. https://doi.org/10.3354/meps015159.

Pinn EH, Ansell AD (1993) The effect of particle size on the burying ability of the brown shrimp *Crangon crangon*. *Journal of the Marine Biological Association of the United Kingdom* 73, 365-377. https://doi.org/10.1071/S0025315400032926.

Plagmann J (1939) Ernährungsbiologie der Garnele (*Crangon vulgaris* Fabr.). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 2, 113–162. https://doi.org/10.1007/bf02253516.

Rauschenplat E (1901) Über die Nahrung von Tieren aus der Kieler Bucht. PhD thesis, Kiel University, Germany.

Reiser S, Herrmann J-P, Temming A (2014a) Thermal preference of the brown shrimp (*Crangon crangon*, L.) determined by the acute and gravitational method. *Journal of Experimental Marine Biology and Ecology* 461, 250-256. https://doi.org/10.1016/j.jembe.2014.08.018.

Reiser S, Herrmann J-P, Neudecker T, Temming A (2014b) Lower thermal limits of the brown shrimp (*Crangon crangon*, L.). *Marine Biology* 161, 447-458. https://doi.org/10.1007/s00227-013-2350-1.

Redant F (1984) An indexed bibliography on the common shrimp, *Crangon crangon* (L.), complementary to Tiews 1967. *International Council for the Exploration of the Sea Committee Meeting* (Shellfish Committee) K2, 1-34.

Saborowski R, Schatte J, Gimenez L (2012) Catalytic properties and polymorphism of serine endopeptidases from the midgut gland of the brown shrimp *Crangon crangon*. *Marine Biology* 159, 1107-1118. https://doi.org/10.1007/s00227- 012-1890-0.

Saborowski R, Paulischkis E, Gutow L (2019) How to get rid of ingested microplastic fibers? A straightforward approach of the Atlantic ditch shrimp *Palaemon varians*. *Environmental Pollution* 254, 113068. https://doi.org/10.1016/j.envpol.2019.113068.

Schatte J, Saborowski R (2006) Change of external sexual characteristics during consecutive moults in *Crangon crangon* L. *Helgoland Marine Research* 60, 70–73. https://doi.org/10.1007/s10152-005-0013-4.

STECF (2016). *Scientific technical and economic committee for fisheries-the 2016 annual economic report on the eu fishing fleet (STECF 16–11)* (p.472). Luxembourg: Publications Office of the European Union.

Tiews K (1970) Synopsis of biological data on the common shrimp *Crangon crangon* (L.). FAO Fisheries Reports 4, 1167-1223.

van der Veer HW, Bergman MJN (1987) Predation by crustaceans on newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Marine Ecology Progress Series* 35, 203-215. https://doi.org/10.3354/meps035203.

Wang ZB, Hoekstra P, Burchard H, Ridderinkhof H, Se Swart HE, Stive MJF (2012) Morphodynamics of the Wadden Sea and its barrier island system. *Ocean and Coastal Management* 68, 39-57. https://doi.org/10.1016/j.ocecoaman.2011.12.022

Wilcox JR, Jeffries HP (1974) Feeding habits of the Sand shrimp *Crangon septemspinosa*. *Biological Bulletin* 146, 424-434. https://doi.org/10.2307/1540416.