Macro-Autoradiographic Studies on North Sea Sediment Bacteria

M. Rieper

Biologische Anstalt Helgoland, D-2192 Helgoland, Federal Republic of Germany

ABSTRACT: Using 14C-labelled substrates it was shown that > 80% of the saprophytic bacteria populations of North Sea sublittoral and littoral sediments have uptake mechanisms for glucose, glucosamine, sodium acetate and aspartic acid. One third are able to utilize glycollic acid whereas only a small fraction degrades fat, phenol and uric acid. Yellow and orange pigmented colonies frequently occur. The numbers of saprophytic bacteria lie within the range of 10^4-10^6 (g dry sediment)^{-1}, with the highest amounts found in the sublittoral sediments with the finest mean particle size. On the beach the greatest amounts of bacteria were found in the mudflats as opposed to the beach slope. There was no apparent correlation between the distribution of the saprophytic bacteria and the meiofauna present in these sediments.

INTRODUCTION

The studies described in this work were undertaken in order to investigate the different physiological groups as well as amounts of saprophytic bacteria available as potential food sources for the meiofauna in different sediment habitats. It has already been shown in laboratory experiments that meiofauna (commonly referring to small sediment-dwelling metazoans which pass a 1 mm sieve but are retained by a 40 μm sieve), such as nematodes and copepods, ingest large quantities of bacteria (Duncan et al., 1974; Brown and Sibert, 1977) but are also able to grow and reproduce on an exclusive diet of bacteria (Rieper, 1978). In order to meet their nutritional requirements in nature, it is probable that many meiofauna animals depend on bacteria and some may have developed unusual mechanisms to ensure a continuous food supply (Gerlach, 1978; Riemann and Schrage, 1978; Hicks and Grahame, 1979). ZoBell and Feltham (1942, p. 76) stated: "It is believed that detailed observations on the numbers and kinds of bacteria in localized areas may often help to explain the presence or absence of the fauna and flora of these areas."

Microbiological investigations were carried out in 1977–1978 on the uppermost layers of marine sediments – where not only the highest bacteria numbers but also the greatest meiofauna densities may be found – from different biotopes in the North Sea. These included various sublittoral sediments near the island of Helgoland (Fig. 1) and a tidal sandy beach including the mudflats of the island Sylt (Fig. 2). Sampling areas were chosen in which the meiofauna and other properties of the sediments had already been investigated (Schmidt, 1968, 1969; Stripp, 1969a, b; see also Weyland, 1967; Hickel and Gunkel, 1968; Westheide, 1968; Rheinheimer, 1977 for earlier studies on North Sea sediment bacteria). In addition to the quantitative investigations on the saprophytic bacteria with the spread plate method, macro-autoradiographic studies were carried out to determine the occurrence and distribution of the different physiological types of bacteria according to their substrate preferences. This represents the first time that the macro-autoradiographic method has been used with sediment bacteria.

MATERIAL AND METHODS

Description of the Study Areas and Sampling Procedures

Helgoland

From January 1977 to February 1978 monthly samples were taken from sublittoral sediments at 3 stations near Helgoland by means of a box grab. Approximately 100 g fresh sediment were removed from the uppermost 2 cm of the surface and stored in a cool place on board the research vessel "Uthörn" until...
further use. The maximum time interval from sampling until return to the laboratory was 3 h. Immediately upon return the samples were diluted and spread plates prepared. The following descriptions of the sediments are according to analyses made by Stripp (1969a), whereby our Stations 1, 2 and 3 correspond to Stripp’s original designations S, AH and H 2, respectively. Decca navigation was used to locate the stations.

Station 1: 54° 15.6’ N, 7° 44.8’ E, depth 33 m.
Sediment analysis: sandy silt, median grain size 92 μm.

Station 2: 54° 09.1’ N, 7° 53.5’ E, depth 49 m.
Sediment analysis: heterogeneous fine to coarse sand, median grain size 345 μm.

Station 3: 54° 06.1’ N, 7° 59.2’ E, depth 30 m.
Sediment analysis: heterogeneous fine sand and mud, median grain size 72 μm.

List/Sylt

Samples from the sandy beach at List/Sylt were taken at maximum low tide at the following stations (Fig. 3): (1) zero mark, point at which the beach slope joins the mudflat area; (2) 10 m mudflat; (3) 25 m mudflat; (4) 10 m on the beach slope. The study area is located directly below the old research station (“Haus C”) of the Biologische Anstalt Helgoland (Litoralstation). Samples were taken from the uppermost 2 cm of
the sediment surface. Since the distance from the beach to the laboratory was very short, the samples could be treated immediately. Sediments at all stations are composed of relatively detritus-poor loose quartz sand. Approximately 70% of the sand grains have a size between 350–700 μm (Westheide, 1968).

**Determining the Numbers of Saprophytic Bacteria**

The spread plate method was used to determine the numbers of viable saprophytic bacteria in the sediment samples (Gunkel and Rheinheimer, 1968). From the original samples 2 cm³ fresh sediment were removed by means of a sterile syringe which had been cut off at one end. This was added to 98 ml autoclaved aged seawater and distilled water at a mixture of 3:1. All samples were shaken vigorously by hand for 2 min, since the commonly used ultra-turrax method (Gunkel, 1974) was unsuitable for sediments containing very coarse sand and shell fragments. From appropriately diluted samples 0.1 ml aliquots were inoculated aged seawater prepared with medium 2216 E (Oppenheimer and ZoBell, 1952). The plates were incubated 14 days at 20 °C. The two most suitable dilutions were used in the final colony counts. Dry weights were determined from aliquots of the same sediment samples which were used for the saprophytic bacteria determinations.

Temperature measurements were made on samples of surface water at the stations near Helgoland, and on the moist beach sand at List from where the samples were taken.

**Macro-Autoradiography**

The macro-autoradiographic method of Hoppe (1974, 1977) was used in order to determine the physiological groups of active, saprophytic bacteria colonies. The technique was modified by raising the salinity of the media from 15% to 24% for marine bacteria. The following ¹⁴C-labelled substrates were used in the investigations: glucose, aspartic acid, sodium acetate, glucosamine, glycerol tripalmitate, phenol, uric acid, and glycollic acid (obtained from Amersham Buchler, Braunschweig, FRG). From sediment samples diluted as above, 10 ml aliquots were filtered through 0.2 μm membrane filters. The filters were then pre-incubated 5–6 d at 20 °C on pads soaked in liquid ZoBell 2216E medium until colonies were clearly visible; they were then transferred to filter paper discs moistened with 0.5 μCi (= 0.75 ml) ¹⁴C-substrate. After 2 d incubation at 20 °C with the labelled substrates, the membrane filters were carefully washed to remove excess substrate, dried overnight at room temperature, and then exposed to X-ray film for 2 d in a light-proof box. The developing and washing procedures are described in Hoppe (1974).

The black spots on the film correspond to bacteria colonies on the membrane filters which were able to utilize a given substrate. Thus the percentage of saprophytic bacteria with uptake properties for that substrate can be calculated. Special attention was given to pigmented colonies and their substrate preferences. To facilitate counting, the membrane filters were later stained with erythrosin (2% erythrosin in a 5% phenol solution) and dried overnight at room temperature.

**RESULTS**

**Numbers of Saprophytic Bacteria**

**Helgoland**

The numbers of saprophytic bacteria found in the different sediments from 3 stations near Helgoland are...
shown in Figure 4 and Table 1. The largest amounts of bacteria are found at Station 3, where the sediment is composed mainly of very fine sand and mud and has the smallest median grain size. At Station 2, where the sediment consists predominantly of coarse sand and shell fragments, the bacteria counts were lower than at Station 3, often by a factor of ten. The lowest numbers were found at Station 1 which has a silty sand sediment. The mean values for a sampling period of 14 months are $2.5 \times 10^6$ (g dry sediment)$^{-1}$ for Station 3, followed by $0.4 \times 10^6$ g$^{-1}$ for Station 2 and $0.3 \times 10^6$ g$^{-1}$ for Station 1. In general, the amounts of saprophytic bacteria are higher during the warmer months of the year and lower from November to March, although considerable fluctuations occur independent of the water temperature (Table 3). The proportion of pigmented bacteria colonies on the agar plates fluctuates between 2 and 8% (Fig. 5). Maxima occur in June–July and October–November. At these times the majority of the bacteria colonies found on the agar plates were yellow or orange; this points to a high bacteria population density consisting of only a few species. Besides orange and yellow forms and colors ranging between yellow-orange and ochre, also red, pink and brown forms were found but much less frequently. Colonies with other pigmentation were rare.

Generally speaking, considering some differences in the methods employed, the results pertaining to the numbers of saprophytic bacteria are on the same order

Table 1. Total saprophytic bacteria numbers for the uppermost sediment layers at the Stations 1, 2 and 3 near Helgoland, expressed for 1 g dry sediment and for 1 cm$^3$ fresh sediment, respectively

<table>
<thead>
<tr>
<th>Date</th>
<th>Station 1</th>
<th>1 g</th>
<th>1 cm$^3$</th>
<th>Station 2</th>
<th>1 g</th>
<th>1 cm$^3$</th>
<th>Station 3</th>
<th>1 g</th>
<th>1 cm$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan. 24, 1977</td>
<td>13 700</td>
<td>22 300</td>
<td>545 000</td>
<td>698 000</td>
<td>78 500</td>
<td>123 000</td>
<td>33 800</td>
<td>806 000</td>
<td>98 800</td>
</tr>
<tr>
<td>Mar. 1, 1977</td>
<td>228 000</td>
<td>401 000</td>
<td>78 500</td>
<td>123 000</td>
<td>33 800</td>
<td>806 000</td>
<td>98 800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mar. 15, 1977</td>
<td>51 600</td>
<td>78 800</td>
<td>27 000</td>
<td>33 800</td>
<td>806 000</td>
<td>98 800</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr. 19, 1977</td>
<td>324 000</td>
<td>512 000</td>
<td>560 000</td>
<td>823 000</td>
<td>2 080 000</td>
<td>1 623 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 11, 1977</td>
<td>7 200</td>
<td>11 600</td>
<td>134 000</td>
<td>199 000</td>
<td>1 900 000</td>
<td>1 681 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 21, 1977</td>
<td>431 000</td>
<td>721 000</td>
<td>1 329 000</td>
<td>2 200 000</td>
<td>1 839 000</td>
<td>1 600 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 21, 1977</td>
<td>110 000</td>
<td>201 000</td>
<td>324 000</td>
<td>505 000</td>
<td>1 541 000</td>
<td>1 125 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug. 11, 1977</td>
<td>1 516 000</td>
<td>2 850 000</td>
<td>1 027 000</td>
<td>1 725 000</td>
<td>4 697 000</td>
<td>4 650 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept. 20, 1977</td>
<td>106 000</td>
<td>173 000</td>
<td>324 000</td>
<td>475 000</td>
<td>1 250 000</td>
<td>1 025 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 25, 1977</td>
<td>908 000</td>
<td>1 425 000</td>
<td>162 000</td>
<td>238 000</td>
<td>18 240 000</td>
<td>11 680 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nov. 21, 1977</td>
<td>11 400</td>
<td>21 300</td>
<td>1 069 000</td>
<td>1 850 000</td>
<td>361 000</td>
<td>325 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dec. 7, 1977</td>
<td>4 200</td>
<td>6 000</td>
<td>469 000</td>
<td>568 000</td>
<td>384 000</td>
<td>280 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan. 18, 1978</td>
<td>56 100</td>
<td>90 000</td>
<td>84 500</td>
<td>118 000</td>
<td>429 000</td>
<td>348 000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feb. 21, 1978</td>
<td>32 100</td>
<td>50 000</td>
<td>71 400</td>
<td>108 000</td>
<td>650 000</td>
<td>413 000</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Total saprophytic bacteria numbers for the uppermost sediment layers at 4 stations from the sandy beach at List/Sylt, expressed for 1 g dry sediment and 1 cm$^3$ fresh sediment, respectively

<table>
<thead>
<tr>
<th>Date</th>
<th>Station 1</th>
<th>1 g</th>
<th>1 cm$^3$</th>
<th>Station 2</th>
<th>1 g</th>
<th>1 cm$^3$</th>
<th>Station 3</th>
<th>1 g</th>
<th>1 cm$^3$</th>
<th>Station 4</th>
<th>1 g</th>
<th>1 cm$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar. 8, 1977</td>
<td>23 200</td>
<td>35 300</td>
<td>111 000</td>
<td>167 000</td>
<td>334 000</td>
<td>497 000</td>
<td>22 700</td>
<td>31 800</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr. 6, 1977</td>
<td>10 000</td>
<td>15 800</td>
<td>71 700</td>
<td>108 000</td>
<td>106 000</td>
<td>169 000</td>
<td>34 200</td>
<td>47 800</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 4, 1977</td>
<td>114 000</td>
<td>184 000</td>
<td>1 048 000</td>
<td>1 630 000</td>
<td>956 000</td>
<td>1 478 000</td>
<td>29 200</td>
<td>41 800</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept. 1, 1977</td>
<td>113 000</td>
<td>193 000</td>
<td>474 000</td>
<td>735 000</td>
<td>186 000</td>
<td>293 000</td>
<td>5 955 000</td>
<td>9 350 000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dec. 5, 1977</td>
<td>80 000</td>
<td>112 000</td>
<td>801 000</td>
<td>1 234 000</td>
<td>866 000</td>
<td>1 334 000</td>
<td>79 100</td>
<td>112 000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Average temperature of surface water from 3 stations near Helgoland from January 1977 to February 1978, and of the moist sand surface at 4 stations from the beach at List/Sylt during five samplings in 1977.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan. 24, 1977</td>
<td>4.1</td>
</tr>
<tr>
<td>Mar. 1, 1977</td>
<td>3.6</td>
</tr>
<tr>
<td>Mar. 15, 1977</td>
<td>3.8</td>
</tr>
<tr>
<td>Apr. 19, 1977</td>
<td>5.2</td>
</tr>
<tr>
<td>May 11, 1977</td>
<td>7.8</td>
</tr>
<tr>
<td>June 21, 1977</td>
<td>11.2</td>
</tr>
<tr>
<td>July 21, 1977</td>
<td>15.1</td>
</tr>
<tr>
<td>Aug. 11, 1977</td>
<td>15.7</td>
</tr>
<tr>
<td>Sept. 20, 1977</td>
<td>15.7</td>
</tr>
<tr>
<td>Oct. 25, 1977</td>
<td>13.8</td>
</tr>
<tr>
<td>Nov. 21, 1977</td>
<td>10.0</td>
</tr>
<tr>
<td>Dec. 7, 1977</td>
<td>7.9</td>
</tr>
<tr>
<td>Jan. 18, 1978</td>
<td>4.5</td>
</tr>
<tr>
<td>Feb. 21, 1978</td>
<td>2.8</td>
</tr>
<tr>
<td>Mar. 3, 1977</td>
<td>7.3</td>
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<tr>
<td>Apr. 6, 1977</td>
<td>7.8</td>
</tr>
<tr>
<td>May 4, 1977</td>
<td>11.5</td>
</tr>
<tr>
<td>Sept. 1, 1977</td>
<td>19.1</td>
</tr>
<tr>
<td>Dec. 5, 1977</td>
<td>0.15</td>
</tr>
</tbody>
</table>

of magnitude as those found by Weyland (1967) and Hickel and Gunkel (1968) during earlier investigations on North Sea sediment bacteria. In samples taken from sediments near the stations described here, Weyland (1967) also found the highest numbers of saprophytic bacteria in muddy sediments \((6.4 \times 10^6 \text{ ml}^{-1})\) compared to those in silty sand \((1.0 \times 10^6 \text{ ml}^{-1})\) and in coarse sand \((0.1 \times 10^6 \text{ ml}^{-1})\).

As in sublittoral sediments near Helgoland, the numbers of saprophytic bacteria occurring in sands from mudflats and beach slope at List/Sylt generally lie within the range of \(10^4\) to \(10^6\) (g dry sediment\(^{-1}\)) (Fig. 6 and Table 2). The highest numbers of bacteria were found at Stations 2 and 3, both of which lie in the mudflat area, where the bacteria counts were at times greater than those on the lower and middle beach slope by a factor of ten or more. This confirms earlier results of Westheide (1968) who also found the maximum numbers of saprophytic bacteria in the mudflats of List compared to those on the lower beach slope. The relatively high value of over 6 million colonies g\(^{-1}\) at Station 4 in September 1977 may be due to a local high concentration, and is not representative for the area. It should be mentioned here that higher values have been found in surface sediments from the supralittoral zones of North Sea beaches: values ranging from \(10^6\) to \(10^7\) (cm\(^3\) fresh sediment\(^{-1}\)) have been found by Westheide (1968) and Rheinheimer (1977). Using fluorescence microscopy on a sediment sample from the supralittoral at St. Peter-Ording, Weise and Rheinheimer (1979) found total bacteria counts of \(10^8\) (cm\(^3\) fresh sediment\(^{-1}\)). Since sediment samples from List were taken only 5 times during the year 1977, a clear seasonal cycle cannot be described. The numbers of saprophytic bacteria in March and April were generally lower than those occurring in May, September and December. The percentage of pigmented bacteria colonies (Fig. 7) was higher in December than in the other months. From samples taken at all 4 stations in December 1977, more than half of the bacteria colonies

![Fig. 5. Percentage of pigmented bacteria colonies of the total saprophytic bacteria occurring in the same samples](image5)

![Fig. 6. Numbers of saprophytic bacteria (g dry sediment\(^{-1}\)) found in samples taken from the sandy beach at List/Sylt (spread plate method)](image6)

![Fig. 7. Percentage of pigmented bacteria colonies of the total saprophytic bacteria occurring in the same samples](image7)
Table 4. Proportion of total saprophytic bacteria populations from sublittoral sediments near Helgoland which are able to utilize a given $^{14}C$-labelled substrate. Maximum and minimum values, as well as the mean (in parentheses), are given for all samples taken.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Sta. 1 (Sandy silt)</th>
<th>Sta. 2 (Coarse sand)</th>
<th>Sta. 3 (Very fine sand, mud)</th>
</tr>
</thead>
</table>
| Glucose        | 94–100 %  
  (99)       | 87–100 %  
  (97)       | 88–100 %  
  (97)       |
| Glucosamine    | 90–100 %  
  (97)       | 86–100 %  
  (95)       | 90–100 %  
  (97)       |
| Sodium acetate | 88–100 %  
  (94)       | 31–99 %  
  (85)       | 94–100 %  
  (97)       |
| Aspartic acid  | 40–100 %  
  (87)       | 44–99 %  
  (81)       | 42–99 %  
  (85)       |
| Glycollic acid | 0–66 %  
  (32)       | 0–60 %  
  (35)       | 11–72 %  
  (33)       |
| Glycerol tripalmitate | 0–26 %  
  (11)       | 5–34 %  
  (15)       | 2–25 %  
  (16)       |
| Uric acid      | 3–25 %  
  (10)       | 0–16 %  
  (8)        | 3–21 %  
  (8)        |
| Phenol         | 0–27 %  
  (6)        | 1–9 %  
  (4)        | 2–13 %  
  (6)        |

Table 5. Proportion of total saprophytic bacteria populations from sandy littoral sediments at List/Sylt which are able to utilize a given $^{14}C$-labelled substrate. Maximum and minimum values, as well as the mean (in parentheses), are given for all samples taken.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Sta. 1 (Bottom slope)</th>
<th>Sta. 2 (10 m mudflat)</th>
<th>Sta. 3 (25 m mudflat)</th>
<th>Sta. 4 (10 m slope)</th>
</tr>
</thead>
</table>
| Glucose        | 99–100 %  
  (100)      | 96–100 %  
  (99)       | 98–100 %  
  (99)       | 97–100 %  
  (99)       |
| Sodium acetate | 85–100 %  
  (94)       | 91–100 %  
  (96)       | 94–100 %  
  (96)       | 89–100 %  
  (96)       |
| Glucosamine    | 81–100 %  
  (92)       | 90–98 %  
  (95)       | 88–90 %  
  (89)       | 77–92 %  
  (87)       |
| Aspartic acid  | 52–100 %  
  (82)       | 59–98 %  
  (81)       | 83–93 %  
  (90)       | 93–98 %  
  (96)       |
| Glycollic acid | 17–59 %  
  (36)       | 16–42 %  
  (29)       | 20–49 %  
  (32)       | 20–49 %  
  (38)       |
| Uric acid      | 11–31 %  
  (22)       | 7–15 %  
  (12)       | 8–14 %  
  (11)       | 6–20 %  
  (13)       |
| Phenol         | 0–4 %  
  (2)        | 0–14 %  
  (5)        | 0–10 %  
  (4)        | 0–27 %  
  (4)        |
| Glycerol tripalmitate | 2–5 %  
  (4)        | 1–5 %  
  (3)        | 3–4 %  
  (4)        | 2–11 %  
  (7)        |

on the agar plates were pigmented yellow or orange. Brown, pink, red and violet colonies occurred less frequently; other colors were rare. The highest proportions of pigmented colonies were found at Station 4 on the middle beach slope zone which was exposed longest during the change of the tide.

**Macro-Autoradiographic Studies on the Bacteria Populations**

The percentage of bacteria from the Helgoland sediments which are able to utilize a given labelled substrate are listed in Table 4. The maximum and minimum as well as the average values (in parentheses) for the period investigated are given.* The order of preference for the substrates shown by the bacteria according to their nutritional demands is as follows: glucose and glucosamine, average uptake values all above 95 %; sodium acetate, over 85 % uptake, followed by

* In the case of glycerol tripalmitate measurements were made only during the 8 months between August 1977 and February 1978; for phenol, uric acid and aspartic acid 11 monthly samples were taken, and 12 for all remaining substrates.
aspartic acid (70–90%), glycolic acid 32–35%, with strong fluctuations regardless of station and season; glycerol tripalmitate, 11 to 16%, uric acid, 8 to 10%, phenol, 4 to 6%. The fluctuations occurring from one sampling period to the next were too great to determine if significant differences were present in the substrate uptake by bacteria in different sediments. No pronounced seasonal cycle was recognized, although the uptake values for uric acid and aspartic acid tended to be higher during the colder months, particularly in silty sand (Station 1) and coarse sand sediments (Station 2). The unusually low uptake values for sodium acetate at Station 2 in April and May may have been due to local disturbances at the sediment surface.

The substrate preferences of bacteria from the beach at List are similar to those from the sublittoral near Helgoland (Table 5). Average uptake values for glucose and sodium acetate were between 94 and nearly 100% of the saprophytic bacteria populations. A relatively high percentage was also to utilize glycosamine (87–95%) and aspartic acid (81–96%), whereby the values for glucosamine, a component of chitin, were less than those found for the Helgoland sediment bacteria. The highest proportion of the bacteria from the beach at List which were able to utilize aspartic acid (> 96%) occurred on the middle beach slope at Station 4, compared to those at the bottom of the slope or in the mudflat area. Glycolic acid, an extracellular product of many algae, was taken up by approximately 1% of the bacteria in all sediments studied. Uric acid (excreted by birds) was utilized by a greater proportion of the bacteria from List (11–22%) than those from the sublittoral sediments near Helgoland. The percentage of phenol-degrading bacteria both from List and Helgoland remained relatively small (2–13%) with the highest values found in samples from the middle beach slope. The substrate which was taken up by the smallest percentage of the bacteria from List was glycerol tripalmitate (fat) with average values of only 3–7% of the saprophytic bacteria population; the values determined for the sublittoral sediments near Helgoland, on the other hand, were 2 to 5 times greater.

Using the macro-autoradiographic method, Hoppe (1974) found that the proportions of the saprophytic bacteria populations in the water of the Kiel Fjord (western Baltic Sea) which were able to utilize uric acid, fat, phenol and sodium acetate decrease with increasing distance from the shore. With regard to the present investigations on North Sea sediment bacteria, however, this effect was not noticeable (considering the stations near Helgoland as shore-distant), although it is possible that the strong fluctuations in the uptake values could have masked small changes occurring in the bacteria populations. The percentages of physiological groups of saprophytic bacteria found in the Baltic

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Glucose</th>
<th>Aspartic acid</th>
<th>Sodium acetate</th>
<th>Glucosamine</th>
<th>Glycerol</th>
<th>Tripalmitate</th>
<th>Phenol</th>
<th>Uric acid</th>
<th>Glycolic acid</th>
</tr>
</thead>
<tbody>
<tr>
<td>List</td>
<td>+</td>
<td>+</td>
<td>none found</td>
<td>+</td>
<td>+</td>
<td>none found</td>
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<td>+</td>
</tr>
<tr>
<td>Helgoland</td>
<td>+</td>
<td>+</td>
<td>none found</td>
<td>+</td>
<td>+</td>
<td>none found</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
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<td>+</td>
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<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Helgoland</td>
<td>+</td>
<td>+</td>
<td>none found</td>
<td>+</td>
<td>+</td>
<td>none found</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 6. Utilization of labelled substrates by pigmented bacteria from a sandy beach at List/Sylt and from sublittoral sediments near Helgoland. + positive, — negative, (+) weak positive.
Sea water by Hoppe (1974) are on the whole comparable to those reported here for North Sea sediments.

As shown in Table 6, the most versatile pigmented bacteria colonies found in samples from the sublittoral sediments were among those with orange or yellow-orange and pink colors. These were able to take up all 8 different substrates tested. This also applies to the samples from the sandy beach at List. In general, comparing these two biotopes, the pigmented bacteria colonies from the three Helgoland stations demonstrate greater uptake properties for the labelled substrates than those from List. Various brown pigmented bacteria found in the sublittoral sediments could also utilize all the substrates, whereas those of the same color group from List could not degrade glycerol tripalmitate (fat) or phenol.

**DISCUSSION**

If many representatives of the meiofauna play a large role as consumers of bacteria in nature, as suggested by Fenchel and Jørgensen (1977), the question arises as to what kinds of bacteria are available as food. The results of macro-autoradiographic studies on North Sea littoral and sublittoral sediments have shown that the saprophytic bacteria on the meiofauna 'menu' have the following characteristics: over 80% have uptake mechanisms for glucose, glucosamine, sodium acetate and aspartic acid. Approximately 1/3 can utilize glycolytic acid; fewer numbers are able to degrade fat, phenol and uric acid. Bacteria which form yellow or orange pigmented colonies on agar occur frequently.

The numbers of saprophytic bacteria present range from $10^4$ to $10^8$ (g dry sediment)$^{-1}$ or (cm$^2$ fresh sediment)$^{-1}$, whereby the greatest concentrations are reached in sublittoral sediments consisting of very fine sand and mud. Relatively high amounts of bacteria are also available in coarser sublittoral sediments as well as in the mudflat zones of a sandy beach, while the smallest numbers are found on the lower and middle beach slope.

Although the physiological groups of saprophytic bacteria considered as a potential food source remained essentially the same in the sediments studied, the differences in the meiofauna populations were considerable. In the sublittoral sediments over 90% of the meiofauna present consisted of nematodes (Juario, 1975). In the sandy beach areas, on the other hand, the meiofauna is composed primarily of copepods, nematodes and tardigrades, all of which show definite preferences for certain zones of the beach slope or mudflats (Schmidt, 1968, 1969). Comparing available data on the meiofauna from these areas (Schmidt, 1968, 1969; Stripp, 1969a, b; Juario, 1975; Mielke, 1976), the greatest individual densities do not occur where the maximum numbers of saprophytic bacteria are found.

Thus, although high concentrations of bacteria are available as food, the distribution of the meiofauna may not be correlated to the kinds and numbers of saprophytic bacteria present in the sediments. It is possible, however, that the macro-autoradiographic method is not sensitive enough to detect small differences occurring within the bacteria populations, which may be of importance to the meiofauna. If so, the isolation and identification of as many bacteria as possible from a given sediment and the determination of their proportion of the bacterial biomass may be necessary, as well as laboratory experiments on the selective feeding of meiofauna using different bacteria strains, such as those currently here in progress.

**Acknowledgements.** Sincere thanks are extended to Professor Dr. G. Rheinheimer (Kiel) and to Dr. W. Gunkel (Helgoland) for critical reading of the manuscript, and to Dr. H.-G. Hoppe (Kiel) for helpful comments on the macro-autoradiographic method.

**LITERATURE CITED**


This paper was presented by Dr. W. Gunkel; it was accepted for printing on October 19, 1979.