Helgol Mar Res (2002) 56:159–168
DOI 10.1007/s10152-002-0111-5

ORIGINAL ARTICLE

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# Temporal, spatial and substrate-dependent variations of Danish hard-bottom macrofauna

Received: 16 October 2001 / Accepted: 13 May 2002 / Published online: 16 July 2002


**Abstract** Detailed knowledge of the Danish hard-bottom fauna is at present limited because of sampling problems. In this study, two different sampling units were used to yield quantitative results of the fauna on two stone reefs in Kattegat: natural holdfasts of *Laminaria digitata* and plastic pan-scourers imitating the holdfasts. On the two reefs a total of 135 taxa (102 species) were identified, representing 12 phyla. One species, the bryozoan *Cribrilina cryptooecium*, has not previously been recorded in Denmark. The fauna was characterized by a mixture of a large number of rare species, yielding high values on the Shannon-Wiener diversity index, and it showed a high degree of spatial and temporal variation. ANOSIM analyses showed a significant difference in species compositions between both sampling location, time and substrate type. The plastic pan-scourers proved to be a valuable substrate for quantitative investigations of the fauna. In contrast, the *Laminaria* holdfasts were too small and variable to be suitable for such studies.

**Keywords** Hard-bottom substrates · Macrofauna · Temporal and spatial variation · Kelp holdfasts · Kattegat

## Introduction

Most of the natural hard substrates in the inner Danish seas are glacial deposits of boulders, stones and gravel forming a large number of reefs. These hard-bottom habitats house a much more diverse fauna than the surrounding soft and sandy bottom (Thorson 1968). Recently, several Danish reefs have been designed as EEC Habitat Areas that are to be included in the national marine monitoring programme.

The Kattegat and Belt Sea waters constitute a transition zone between the brackish Baltic Sea and the highly saline North Sea. Mean annual salinity at 10 m depth varies from about 12‰ in the western Baltic to about 32‰ in the northern part of Kattegat (Rasmussen 1995). As a consequence the number of species increases northwards through Kattegat (Hylleberg 1978).

Detailed knowledge of the hard-bottom fauna is limited at the present time because of sampling problems. Stone reefs are characterized by substantial local variation, physically as well as biologically, which makes quantitative sampling difficult. The last comprehensive investigation of the Danish hard-bottom fauna was undertaken more than a hundred years ago by Petersen (1893). He used a triangle dredge to provide qualitative data from the inner Danish waters. Few studies have investigated the fauna quantitatively (Rasmussen 1973; Nielsen et al. 1997; Wernberg-Møller et al. 1998).

To overcome the practical difficulties of sampling hard-bottom epifauna, holdfasts of different species of large brown algae can be used as representative sampling units. They constitute small habitat islands on the bottom where they provide shelter for a large variety of marine invertebrates. Holdfasts have been used in baseline studies and monitoring programmes of hard-bottom communities throughout the world (Jones 1969; Edwards 1980; Sheppard et al. 1980; Ojeda and Santelices 1984; Smith and Simpson 1992; Smith 1996; Smith et al. 1996).

However, natural holdfasts are variable in size and structure, and samples can be difficult to compare. In contrast, artificial substrates in the form of plastic pan-scourers can easily be standardized and have also been found suitable for investigating hard-bottom invertebrate communities (Schoener 1974; Myers and Southgate 1980; Gee and Warwick 1996). The scourers form a

Communicated by E. Rachor

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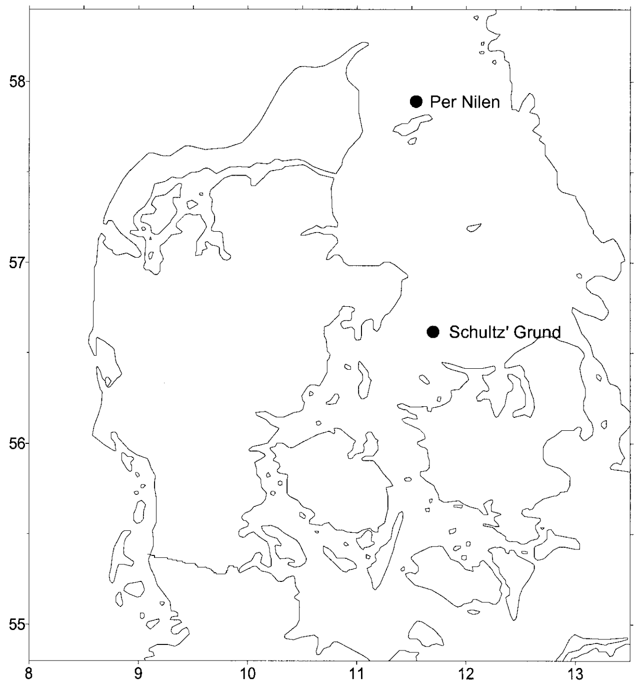


**Fig. 1** Sampling localities

loose network of thin plastic filaments that give shelter to smaller invertebrates in the same way as the holdfast branches. At a given external volume the thin filaments of the scourers leave much more free space within the structure compared with *Laminaria* holdfasts. On the other hand, the thin filaments might be more difficult to use as a substrate for sessile animals than the broader branches of the holdfasts. Furthermore, they make up a suitable sample size and are cheap and easy to handle.

In the present study, we wished to evaluate the faunal communities of two Danish stone reefs. The fauna were sampled twice during the summer and species compositions were compared quantitatively. The species composition of the different sampling sites and times were expected to be different due to temporal and spatial population dynamics and changing physical conditions. Two different sampling methods were used: natural holdfasts of *Laminaria digitata* and plastic pan-scourers imitating the holdfasts. The suitability of the two substrate types for such studies was evaluated and compared.

## Methods

### Sampling sites

Two reefs in Kattegat were included in the investigation: Per Nilen in the northern part of Kattegat and Schultz's Grund in the southern part (Fig. 1). Boulders dominated the top of both reefs to approximately 9–10 m depth. Below this depth the sediment consisted of a mixture of boulders, gravel and sand on both reefs. The proportion of fine-grained sediment increased with depth. Per Nilen is partly sheltered by the island Læsø and by a large more or less submerged sandbank west and north of the reef. Schultz's Grund is more exposed, being located in the middle of a deeper channel entering the Great Belt.

Sampling was carried out in June and August 1998 from the Nature and Forest Agency research vessel "*Havternen*". Sites were chosen on each reef that were comparable with respect to depth and boulder cover. All stones larger than 10 cm in diameter were almost completely covered by a mixed brown and red algae multilayered vegetation. Sampling depth was 8–9 m at both sites. A short characterization of the sediment structure and salinity of the two sample sites is given in Table 1.

### Experimental design

In June 1998, 12 *Laminaria digitata* holdfasts were collected on Per Nilen and ten on Schultz's Grund. At the same time ten plastic pan-scourers were left out on each locality for colonization of fauna. In August 1998 another nine holdfasts were sampled on Per Nilen and ten on Schultz's Grund and the plastic pan-scourers were recollected (Table 1).

### Field work

Divers manually sampled the holdfasts as described in Jones (1969). The pan-scourers (diameter 8 cm, height 2 cm, volume 100 ml) were anchored by iron pegs to the sea floor near the growth place of the sampled *Laminaria* populations. A search line was connected between the pan-scourers and underwater buoys reaching 1.5 m up in the water column.

**Table 1** Sampling localities: Sediment composition (percentage of the bottom covered by stones of given sizes), salinity at 9 m depth, sampling design and notation code. Depth at both localities: 8–9 m

| Locality | Per Nilen | | | Schultz's Grund | | |
|---|---|---|---|---|---|---|
| Position | 57°22.74 N, 11°02.57 E | | | 56°09.61 N, 11°11.30 E | | |
| Sediment cover | | | | | | |
| >60 cm | 5% | | | 5% | | |
| 30–60 cm | 15% | | | 25% | | |
| 10–30 cm | 20% | | | 40% | | |
| 5–10 cm | 20% | | | 10% | | |
| 2–5 cm | 15% | | | 15% | | |
| <2 cm and sand | 25% | | | 5% | | |
| Salinity | | | | | | |
| Median | 28.4‰ | | | 20.7‰ | | |
| Range[a] | 21.7–32.7‰ | | | 15.6–29.6‰ | | |
| Sampling date | 06-06-98 | 16-08-98 | 16-08-98 | 02-06-98 | 10-08-98 | 10-08-98 |
| Substrate | Holdfasts | Holdfasts | Pan-scourers | Holdfasts | Holdfasts | Pan-scourers |
| No. of samples | 12 | 9 | 10 | 10 | 10 | 10 |
| Code | PN-6-h | PN-8-h | PN-8-p | SG-6-h | SG-8-h | SG-8-p |

[a] Salinity range 90% of the time

### Laboratory work

On deck, the material was fixed in 4% borax-buffered formalin, and transported to the laboratory where the holdfasts were measured and dissected and the pan-scourers unravelled. The volume of the holdfasts was measured by immersing each one in water and registering the amount of water displaced. The same was done for a few pan-scourers each wrapped in a plastic bag. The associated fauna retained by a 1.0 mm mesh sieve were preserved in 80% ethanol. The fauna were identified to the lowest possible taxonomic level and quantified as far as possible: for the solitary species the number of individuals were counted, and these data constitute the "quantitative data" referred to throughout this paper. The colonial species were recorded as present/absent. These data, together with the presence-/absence-transformed data for the solitary taxa, constitute the so-called "qualitative data".

### Statistical analyses

The "qualitative" and "quantitative" data mentioned above were treated separately in some of the following statistical analyses. Some analyses were therefore run twice: once for the quantitative data including the countings of solitary individuals, but omitting the colonial species, and once for the qualitative data, i.e. including all of the species but transformed to presence/absence.

The programme package PRIMER was used for multivariate statistical analyses (Clarke and Warwick 1994):

*Standardization:*
To cope with the variable holdfast volumes, species abundance data were standardized for all quantitative analyses on holdfasts. Thus the percentage of total abundance (over all species) that was accounted for by each species (Clarke and Warwick 1994) was calculated.

*Transformation:*
The quantitative data were 4th-root-transformed ($\sqrt{\sqrt{x}}$) to balance the contributions from the few very abundant species (mostly juveniles) with the many rare species, some only present with one individual (Smith and Simpson 1992; Clarke and Warwick 1994; Gee and Warwick 1994). Qualitative data were presence/absence-transformed to compare data for colonial and solitary species.

*Similarity*:
Using the standardized and transformed data, Bray-Curtis similarities were computed for every pair of samples (Clarke and Warwick 1994, 1998). The resulting similarity matrix made up the basis for the analyses described next.

Two-way-crossed ANOSIM analyses can be used to test for differences in species composition with respect to two given parameters. However, the present experimental design imvolved the three parameters *Locality*, *Month* and *Substrate*. To handle this, the analysis was run twice, i.e. on the two relevant subsets of the total data matrix. The first run tested for effects of *Locality* and *Month* and the second for effects of *Locality* and *Substrate*. One of the three parameters thus inevitably appeared twice, and this was arbitrarily chosen to be *Locality*. While testing for substrate differences, the plastic pan-scourers were compared to holdfasts collected in August solely, to avoid bias from temporal differences. Similarly, temporal differences were studied using only the results of the holdfasts, so that the interpretations were not confused with effects of substrate differences. Furthermore, the calculations were repeated for quantitative and qualitative data separately.

An MDS-ordination plot revealed the degree of similarity between samples from the different localities, sampling times and substrate types.

To investigate the biodiversity, the Shannon-Wiener diversity index ($H'$) was calculated for each combination of site, time and substrate. Because the index is based on abundances (as well as species numbers), it was calculated solely from the quantitative data.

SIMPER analyses of the pan-scourer data were run for quantitative and qualitative data separately to investigate which species contributed most to similarities and dissimilarities among the samples. The analyses were also used to compare sampling groups by comparing within-group similarities and between-group dissimilarities.

To evaluate the importance of identification level, the original data set (identified to species level) was finally aggregated to family level and exposed to the same statistical analyses.

## Results

### Substrate

The volume of the holdfast branches on Per Nilen varied from 0.5 to12 ml and on Schultz's Grund from 10 to 40 ml. The total volume of the plastic pan scourers was 100 ml. The age of the holdfasts was not determined, but those from Per Nilen were assumed to be younger because of smaller size and fewer branchings.

### Associated fauna

In total, 135 taxa (102 species) were identified, representing 12 phyla: Porifera, Cnidaria, Nemertini, Sipuncula, Bryozoa, Entoprocta, Mollusca, Annelida, Arthropoda, Crustacea,[1] Echinodermata and Chordata. The complete data set is presented in the Appendix. In total, 104 taxa were found on Per Nilen and 89 taxa on Schultz's Grund; 58 taxa (43%) occurred on both localities. Approximately 70% of the found taxa (94) were solitary animals, and 30% (41 taxa) were colonial animals.

The species distributions on overall taxonomic level were quite similar at the different sites, times and localities. The five phyla Annelida, Mollusca, Crustacea, Bryozoa and Cnidaria together contributed nearly 90% of the species. On Per Nilen the Bryozoa was the phylum containing most species, whereas on Schultz's Grund the most species-rich phylum was the Annelida.

### New species record for Danish waters

The bryozoan *Cribrilina cryptooecium* has not previously been recorded in Denmark. *Cribrilina cryptooecium* was found on a few holdfasts from Per Nilen in June and August, and on one holdfast from Schultz's Grund in June. It was not found on any of the plastic pan-scourers. The species is common along all British coasts, and has been reported from arctic Russia and Nova Scotia, but not south of Great Britain (Hayward and Ryland 1979).

### Variation among samples

There were significant differences in fauna composition between the two reef localities using both quantitative and qualitative data (Table 2). The differences are illustrated in the MDS-plot in Fig. 2. The same results were found using data aggregated to family level (not shown).

[1] According to the most recent literature (Hayward and Ryland 1995) the Crustaceans have been assigned a separate phylum rather than being a part of the phylum Arthropoda

**Table 2** Results of the two-way-crossed ANOSIM analyses

| | | Quantitative data | | Qualitative data | |
|---|---|---|---|---|---|
| | | Global *R* | Significance level | Global *R* | Significance level |
| 1. analysis | Locality | 0.682 | <0.05% | 0.820 | <0.05% |
| | Month | 0.429 | <0.05% | 0.289 | <0.05% |
| 2. analysis | Locality | 0.844 | <0.05% | 0.909 | <0.05% |
| | Substrate | 0.675 | <0.05% | 0.770 | <0.05% |

**Table 3** Means of species number and Shannon-Wiener diversity index ($H'$) per sample in each sampling group showing SD. For notation, see Table 1

| | Shannon-Wiener diversity index ($H'$) (Quantitative data) | Mean no. of solitary species (Quantitative data) | Mean no. of all species (Qualitative data) |
|---|---|---|---|
| PN-8-h | 1.41 ± 0.36 | 5.1 ± 2.2 | 10.6 ± 3.2 |
| PN-6-h | 1.56 ± 0.50 | 8.5 ± 5.6 | 15.3 ± 7.1 |
| PN-8-p | 1.96 ± 0.33 | 20.3 ± 2.9 | 29.4 ± 6.2 |
| SG-6-h | 2.17 ± 0.25 | 17.9 ± 3.9 | 24.1 ± 5.0 |
| SG-8-p | 2.24 ± 0.12 | 17.8 ± 3.1 | 23.0 ± 4.5 |
| SG-8-h | 2.44 ± 0.13 | 17.3 ± 3.5 | 24.3 ± 3.9 |
| Mean | 1.97 ± 0.47 | 14.5 ± 6.6 | 21.1 ± 8.0 |

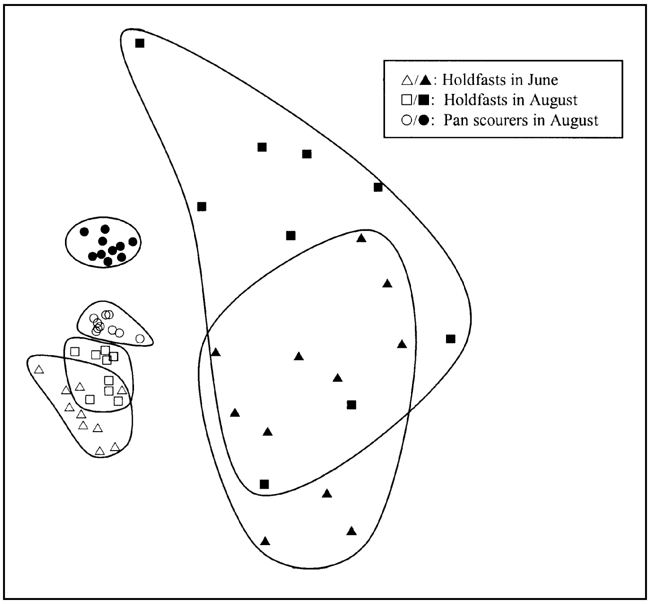


**Fig. 2** MDS-plot of quantitative data, stress = 0.18. *Open symbols* indicate Schultz's Grund, *closed symbols* indicate Per Nilen. Sampling groups are *encircled*

**Table 4** Results of the SIMPER analyses. For notation, see Table 1

| Parameter | Station | Sim.[a] | Dissim.[a] | Sim.[b] | Dissim.[b] |
|---|---|---|---|---|---|
| Locality | PN-8-p | 67 (65) | 48 (48) | 66 | 48 |
| | SG-8-p | 73 (72) | | 73 | |
| Month | PN-6-h | 33 (35) | 77 (69) | 34 | 73 |
| | PN-8-h | 29 (38) | | 34 | |
| | SG-6-h | 56 (50) | 47 (49) | 53 | 48 |
| | SG-8-h | 64 (63) | | 63 | |
| Substrate | PN-8-h | 29 (38) | 76 (74) | 34 | 75 |
| | PN-8-p | 67 (65) | | 66 | |
| | SG-8-h | 64 (63) | 42 (45) | 63 | 43 |
| | SG-8-p | 73 (72) | | 73 | |

[a] Similarities/dissimilarities for each group given for quantitative data followed by qualitative data in brackets. Values are calculated as the average between all samples within each group
[b] Average of similarities/dissimilarities between quantitative and qualitative data. Localities are only compared for pan-scourers because of the systematic differences in holdfast volume

The pan-scourer samples from Per Nilen and Schultz's Grund constitute two clearly distinct groups. Furthermore, the holdfasts of Schultz's Grund are grouped corresponding to sampling time. However, the holdfasts from Per Nilen are scattered over the diagram, illustrating the great variation among these samples.

Holdfasts from Per Nilen also differed from the other samples by showing low numbers of species and low Shannon-Wiener diversities ($H'$=1.41 or 1.56) (Table 3). The highest diversity was found on holdfasts from Schultz's Grund in August (2.44), whereas the highest average number of species was found on pan-scourers from Per Nilen (29.4). The diversity indices of the six sampling groups were significantly different from each other (Kruskal-Wallis test, $K$=37.1, $P$<0.01).

SIMPER analyses for the quantitative and qualitative data showed very similar results (Table 4). In Fig. 3a, b the average values of similarities within groups and dissimilarities between groups are shown for qualitative ($y$) against quantitative ($x$) data. The resulting data cluster closely around the $y$=$x$ line where results from the two data sets would be identical. For simplicity, therefore, average similarity/dissimilarity values between qualitative and quantitative data will be used in the following. The most clearcut trend in the results was that the similarity values within groups differed according to substrate volume (Fig. 3a and Table 4). The average similar-

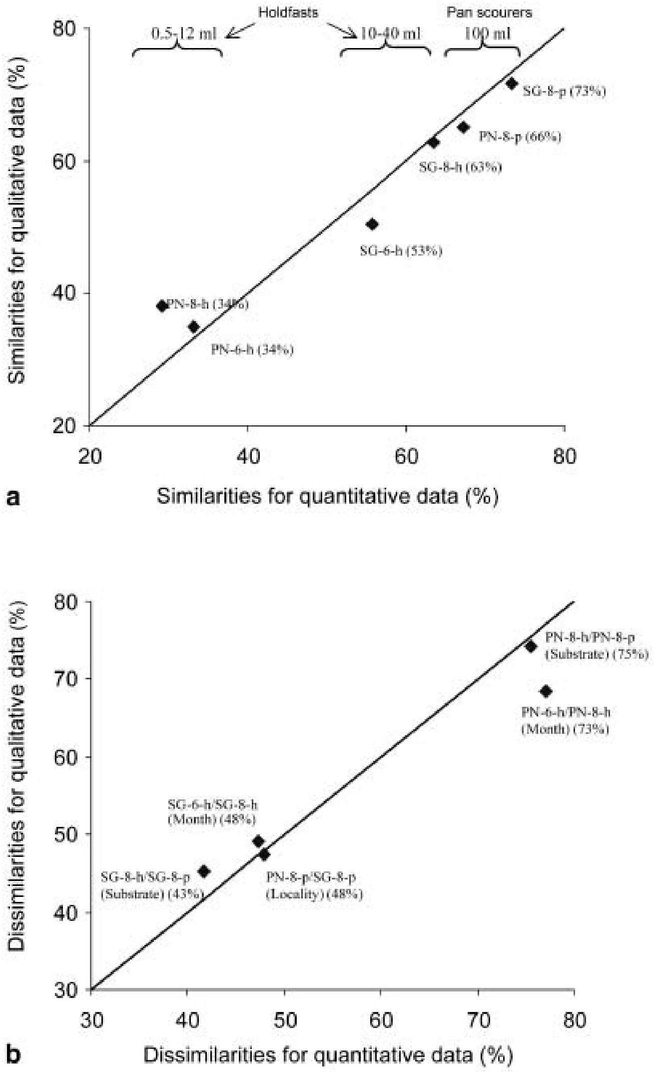


**Fig. 3** **a** Similarities within groups for qualitative against quantitative data; sampling groups shown and range of substrate volume *inset above*. **b** Dissimilarities between groups for qualitative against quantitative data; combinations of sampling groups shown

ities for pan-scourers (100 ml) were 66–73%, for the large holdfasts from Schultz's Grund (10–40 ml) between 53–63% and for the small holdfasts from Per Nilen (0.5–12 ml) 34%.

Comparing the two localities (using only the pan-scourer data), both data groups (PN-8-p, SG-8-p) showed high within-group similarities (66–73%), corresponding to the high substrate volume (Fig. 3a). There was a relatively low dissimilarity of 48% between these two groups (Fig. 3b).

Both months and substrate types were compared for each locality separately, yielding quite different results (Table 4). On Per Nilen the within-group similarities were lower (34–66%) than on Schultz's Grund (53–73%) (Fig. 3a). Correspondingly, the average dissimilarities between the groups were much higher on Per Nilen (73–75%) than on Schultz's Grund (43–48%) (Fig. 3b).

Considering the *quantitative* data, species that were all very abundant on one locality, and almost absent on the other, contributed most to the dissimilarity between localities (data not shown). Some examples were the gastropod *Rissoa* sp., the amphipods *Apherusa bispinosa* and *Corophium bonnelli* and newly settled *Scyphozoa* indet. The same species appeared when the *qualitative* data were investigated, but here a few colonial species also contributed to the dissimilarity, e.g. the bryozoan *Crisia eburnea*, which was found on all pan-scourers from Per Nilen and not elsewhere. Another bryozoan, *Celleporella hyalina*, was recorded from nearly all Schultz's Grund samples, regardless of substrate type, and was absent on Per Nilen.

Aggregation to family level had little effect on the outcome of the analyses. The statistical analyses of the aggregated data set showed very similar results to that of the original data set identified to species level (data not shown). The same pattern of variation between samples was found as well as the same degree of difference between sampling groups.

## Discussion

The present data set makes up the most comprehensive quantitative study to date on the Danish hard-bottom fauna. All macroinvertebrate taxa that could be properly identified were included in the analyses.

In general, hard-bottom fauna in the inner Danish waters and along the Swedish west coast have been poorly described, mainly due to sampling difficulties (see among others (Bergh 1871; Gislén 1930; Thorson 1957, 1979; Nielsen et al. 1997). Most of these studies are qualitative and need extensive adaptations before comparison with the present data set is possible.

Comparable quantitative studies on hard-bottom fauna from other sea areas include only countable species from a few selected phyla (Ojeda and Santelices 1984 in Chile; Smith et al. 1996 in Australia). However, Kluijver (1991) stressed the importance of studying the community as a whole, i.e. including all taxonomic groups. In the present investigation about 30% of the observed species were colonial and would thus have been missed if such a simplification was applied. The resulting data set implies some statistical complications but renders a more complete picture of the local fauna.

The observed fauna consisted of many species with low abundances, and showed considerable temporal and spatial variations in species composition. These results are consistent with studies of macroalgae on the same stone reefs, which also show great species diversity and variability among the algae (Nielsen et al. 1991, 1994, 1997; Dahl et al. 2001). Together, the Danish investigations establish the stone reefs as rich and diverse marine habitats placed as islands on the more widespread soft bottom in the Danish seas.

Two studies of hard-bottom fauna in the nearby German Bight confirm that these habitats do indeed attract a larger number of both common and rare species than soft-bottom habitats (Kluijver 1991; Kühne and Rachor 1996). Both found several animal communities associated with the hard bottoms (see "Animal communities" section below). Other studies of kelp holdfasts from Ireland, England and Chile have found Shannon-Wiener diversity index values ($H'$) of 1.4–2.4, similar to the values found in this study (Edwards 1980, Ireland; Sheppard et al. 1980, England; Ojeda and Santelices 1984, Chile).

## Spatial differences

A highly significant difference between samples from the two localities was established by the ANOSIM analysis (Table 2). In Fig. 2, this difference is visualized in two ways. First, regarding the pan-scourers, samples from Per Nilen and Schultz's Grund constitute two clearly distinct groups, each one closely clustering. Second, regarding the holdfasts, samples from Per Nilen are spread widely over the diagram, while those from Schultz's Grund are closely grouped according to sampling month. The more scattered distribution of samples from Per Nilen is most probably due to the small and variable holdfasts of this locality.

Species numbers and diversity ($H'$) were expected to be higher on Per Nilen because of the higher salinity in the northern part of Kattegat. Considering the plastic pan-scourers only (which were free from volume-caused bias), the total number of species found was indeed higher on Per Nilen (70 taxa) than on Schultz's Grund (48 taxa) (Table 3). In particular, the phylum Bryozoa contributed to this difference with 21 species at Per Nilen in contrast to ten species at Schultz's Grund. However, the mean Shannon-Wiener diversity index ($H'$) on the pan-scourers of Per Nilen (PN-8-p) was lower than on those of Schultz's Grund (SG-8-p). This is caused by the dominance of the gastropod *Rissoa* sp. on Per Nilen.

## Substrate differences

The significant difference between the species composition of the two substrate types (Table 2) is illustrated in Fig. 2. The dense clustering of the pan-scourer samples from both localities contrasts with the slightly more widespread holdfast samples from Schultz's Grund and especially the extremely widespread holdfasts from Per Nilen.

In the SIMPER analyses, the within-group similarities were generally higher for the pan-scourers than for the holdfasts (Fig. 3a). This was probably an artefact of higher substrate volumes and thereby less variation among samples.

The total number of species as well as the Shannon-Wiener diversity index found on each substrate type apparently reflected both the substrate volume and the time spent on the bottom. On Per Nilen, the small, and presumably young, holdfasts comprised fewer species and showed lower $H'$ values (Table 3) than the much larger plastic pan-scourers, indicating the importance of substrate volume. The opposite situation was seen on Schultz's Grund, where the holdfasts actually contained more species than the pan-scourers, and in August also showed a higher $H'$ value than the scourers. This was probably due to the longer time spent on the bottom by the holdfasts (one to several years) compared with the pan-scourers (2 months).

The bryozoan *Amphiblestrum auritum* and the cnidarian *Sagartia troglodytes* were both found in all of the holdfasts from Schultz's Grund and not in any other samples. Maybe the larvae of these species settled patchily elsewhere or maybe they were released during other times of the year than June–August, where the plastic scourers were available as a substrate. However, especially on Per Nilen, most other sessile species were represented on the pan-scourers, indicating that new larvae did actually settle on the artificial substrate during the summer. For most of the species (both sessile and motile) found in this study, reproduction and population dynamics are presently not known in detail.

The *Laminaria* holdfasts sampled in this study turned out to be of such small size (<40 ml) and variable structure that they were unsuitable for quantitative investigations of the fauna. Holdfasts used in other studies in full-saline waters (Jones 1969; Edwards 1980; Sheppard et al. 1980; Ojeda and Santelices 1984) grow up to a capacity of several litres, which makes the individual samples more homogeneous and the resulting data set more statistically reliable.

For many species, the holdfasts are used as a kind of "kindergarten" (Ojeda and Santelices 1984). The juveniles seek protection between the branches of the holdfast until they grow too large. This makes the identification of the holdfast fauna difficult. Larger holdfasts have a greater proportion of adult animals, making the identification easier. The many juveniles also indicate lively population dynamics, where considerable temporal and spatial variation can be expected.

In contrast, the plastic pan-scourers proved to be a valuable substrate for quantitative studies of macroinvertebrates on Danish stone reefs. They attracted a wide variety of invertebrates from the surrounding habitat, representing a subset of the local stone reef fauna. However, the present study showed a significant difference between the fauna composition of the pan-scourers and that of the holdfasts. In contrast to this, Myers and Southgate (1980) showed that plastic pan-scourers quickly (within 1 month) attained a species composition similar to surrounding red algal turfs. Furthermore, they found that at least some species were more uniformly distributed in the artificial sponges than in the surrounding algal vegetation, indicating that a relatively small number of samples was necessary to cover the distribution of the animals. Probably the pan-scourers with a relatively open space between the thin plastic filaments are structurally more similar to red algal turfs than to the compact holdfasts investigated in this study. Also, the red algal turfs are supposed to be faster growing than the holdfasts. Therefore, red algal turfs of similar size as the holdfasts must be younger, making them even more similar to the pan-scourers, which spent only 1 month on the sea floor.

### Temporal differences

The ANOSIM analyses showed a significant difference between the sample groups from June and August. However, Global R (Table 2) was smaller for comparison of *Months* than for *Locality* and *Substrate*, indicating a weaker degree of temporal difference than that of spatial and substrate differences. This is supported by the other statistical analyses, which also showed only weak differences between the two sampling times.

SIMPER analysis for Per Nilen showed rather high dissimilarities between the two months and low within-group similarities for each month. The combination of low similarities within groups and a high dissimilarity among groups indicates a generally high degree of heterogeneity and randomness. This was thus apparently an artefact of the variable and small holdfasts, as was also clear from the widespread appearance of the samples on the MDS-plot.

On Schultz's Grund the opposite trend was seen, showing higher within-group similarities and lower dissimilarities among the two months. This indicates a generally high uniformity of the species composition of holdfasts from Schultz's Grund regardless of sampling time. Again, this was supported by the MDS-plot where all the holdfasts from this locality clustered rather densely together.

### Animal communities

The results did not reveal any clear animal communities dominated by a few species, as has been widely reported from soft-bottom studies (Petersen 1893; Thorson 1968) and from a few hard-bottom studies (Ojeda and Santelices 1984; Kluijver 1991; Kühne and Rachor 1996). Rather the fauna was characterized by a great number of rare species, yielding a high biodiversity.

Supporting this, there were no major deviations between the statistical analyses based on quantitative (abundance) and qualitative (incidence) data. The SIMPER analysis revealed that both the similarities within groups and the dissimilarities between groups were made up of small contributions from a large number of species. This indicated a diverse community with a highly complex structure, where many species were almost equally important for the total species composition. It is true that this trend was amplified by the $\sqrt{\sqrt{x}}$-transformation that was used to balance the contributions from rare and abundant species. However, the results could still be compared to other studies, since most of these use the same or similar transformation of data (Edwards 1980; Kluijver 1991; Smith and Simpson 1992; Gee and Warwick 1994; Smith et al. 1996).

The same patterns of spatial, temporal and substrate-dependent variation appeared in the results regardless of using quantitative or qualitative data as well as using data identified to family or species level. This is because the number of species is nearly equal to the number of families. If this proves to be a general trend, future studies can concentrate on either solitary or colonial species and, furthermore, the time-consuming identification to species level can be eliminated. This is especially of interest in monitoring studies, where cost–benefit relations are of paramount importance.

Knowledge of species composition and dynamics is crucial for a sound management of the Danish hard-bottom habitats. The present study concludes that these habitats are species-rich and diverse localities, but new questions arise: How many – and which – species live at the stone reefs in total, i.e. beyond the holdfast micro-habitats? What are the recruitment, interactions and general dynamics of the fauna? How do the densities and dominance of the different species fluctuate during the year and over several years? Which physical and biological factors are important in determining the composition of these faunal assemblages? And how robust are they to natural or human disturbances? Further studies using a combination of different sampling methods will be necessary in order to answer these questions.

**Acknowledgements** The present study was carried out as a Master project at the Zoological Museum (University of Copenhagen) and the National Environmental Research Institute (Roskilde, Denmark). Among others, we wish to acknowledge the help of the following people: Ole Tendal for supervising the project, Ib Svane for inspiration to sampling design and methods, Steffen Lundsteen, Kim Lundshøj and Jan Damgaard for diving assistance, and Peter Munk and Thomas Wernberg-Møller for valuable comments on the manuscript. We are grateful to the several specialists for taxonomic assistance: Ole Tendal (Porifera, Cnidaria, Sipuncula, Echinodermata, Ascidiacea, Cephalochordata), Godtfred Høpner Petersen (Bivalvia), Danny Eibye-Jacobsen (Annelida), Kathe Jensen, Jørgen Knudsen and Aslak Jørgensen (Gastropoda), Karen Bille Hansen and Claus Nielsen (Bryozoa), Teunis Jansen and Jørgen Olesen (Crustacea), Anne Klitgaard (Pycnogonida) and Steffen Lundsteen (Hydrozoa, Entoprocta). Staff and students at the two institutes have provided valuable discussions and encouragement during the project. The field experiments undertaken in this study comply with the current Danish laws.

## Appendix

### Data set

The collected data show abundance (no) for solitary species and presence (*X*) for colonial species. In total 135 taxa were found.

| | | Per Nilen, June, holdfasts | | | | | | | | | | | | Per Nilen, August, holdfasts | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Porifera | *Leucosolenia botryoides* | X | | | | | | | X | X | X | X | X | X | | | | | | X | | |
| | *Halisarca dujardini* | | | | X | | | | | | | | | | | | | | | | | |
| | *Halichondria panicea* | | | | | | | | X | | | | | | | | | X | X | | X | X |
| Cnidaria | Scyphozoa indet. | | | | | | | | | | | | | | | | | | | | | |
| | Athecata indet. | | | | | | X | | | | | | | | | | | | | | | |
| | *Bougainvillia ramosa* | | | | | X | | | | | X | | | | | | | | X | | | X |
| | *Clava multicornis* | | | | | | | | | | | | | | | | | | | | | |
| | *Eudendrium arbusculum* | | | | | | | X | | | | | | | | | | | | | | |
| | *Opercularella lacerata* | | | | | | | | | | | | X | | | | | | | | | |
| | *Calycella syringa* | | | | | | X | X | | | | | | | | | | | | | | |
| | *Hydrallmannia falcata* | | | X | | X | | | | | | | | | | | | | | | | |
| | *Sertularella rugosa* | X | | | | | | X | | | | | | | | | | | | | | |
| | *Clytia gracilis* | | | | | | | | | | X | | | | | | | | | | | |
| | *Clytia hemisphaerica* | X | | X | | | | | X | X | | X | X | | | | | | | | | |
| | Obeliinae indet. | | | | | | X | | | | | | | | | | | | | | | |
| | *Gonothyraea loveni* | X | | | | | | X | | X | | | | | | | | | | | | |
| | *Obelia geniculata* | X | | | | | | X | | | | X | X | | X | | | | | | | |
| | *Obelia longissima* | | | | | | | | | | | | | | | | | | | | | |
| | *Sagartia troglodytes* | 2 | | 1 | | | | | | | | | | | | | | | | | | 1 |
| | *Sagartiogeton undatus* | | | | | | | | | | | | | | | | | | | | | |
| | *Metridium senile* | | | | | | | | | | | | | | | | | | | | | |
| Nemertea | Nemertea indet. | | | | | | | | | | | | | | | | | | | | | |
| Sipuncula | Sipuncula indet. | | | | | | | | | | | | | | | | | | | | | |
| Mollusca | *Leptochiton asellus* | | | | | 1 | | | | | | | | | 1 | | | | | | | |
| | *Lacuna vincta* | | | | | | | | | | | | | | | | | | | | | |
| | *Littorina littorea* | | | | | | | | | | | | | | | | | | | | | |
| | *Rissoa* sp. | | | | | | | | | | | | | | 1 | 1 | | | 2 | | | 10 |
| | *Onoba semicostata* | | 2 | | | | | | | | | | | | | | | | | | | |
| | *Bittium reticulatum* | | | | | | | | | | | | | | | | | | | | | |
| | *Buccinum undatum* | | | | | | | | | | | | | | | | | | | | | |
| | *Chrysallida obtusa* | | | | | | | | | | | | | | | | | | | | | |
| | *Brachystomia rissoides* | | | | | | | | | | | | | | | | | | | | | |
| | *Diaphana minuta* | | | | | | | | | | | | | | | | | | | | | |
| | *Goniodoris nodosa* | | | | | | | | | | | | | | | | 1 | | | | | |
| | *Acanthodoris pilosa* | | | | | | | | | | | | | | | | | | | | | |
| | *Onchidoris muricata* | | | | | | | | | | | | | | | | | | | | | |
| | *Coryphella verrucosa* | | | | | | | | | | | | | | | | | | | | | |
| | Bivalvia indet. | | | | | | | | | | | | | | | | | | 1 | 1 | | |
| | *Modiolus modiolus* | 4 | 1 | | | | 1 | 2 | | | | | | | | | | | | | 1 | |
| | *Musculus discors* | | 1 | | | 1 | | | | | | | | | | | | | | | | |
| | *Anomia* sp. | | | | 1 | 4 | | | | | | | 1 | | 3 | | | | | 3 | | 4 |
| | *Musculus* sp. | | | | | | | | | | | | | | | | | | | | | |
| | *Mysella bidentata* | | | | | | | | | | | | | | | | | | | | | |
| | *Parvicardium* sp. | | | | | | | | | | | | | 1 | | | | | | | | |
| | *Parvicardium ovale* | | | | | | | | | | | | | | | | | | | | | |
| | *Hiatella arctica* | 13 | 10 | 2 | 7 | 2 | 2 | 5 | 4 | | 1 | | 2 | 1 | 3 | | 2 | 2 | 3 | 1 | 7 | 8 |
| | *Thracia phaseolina* | | | | | | | | | | | | | | | | | | | | | |
| Annelida | *Polychaeta indet.* | | 2 | | | | | | | | | | | | | | | | | | | |
| | *Harmothoe* sp. | | | | | | | | | | | | | | | | | | | | | |
| | *Harmothoe imbricata* | | 1 | | | | | 1 | | | | | | | 1 | | | 1 | 2 | | | |
| | *Lepidonotus squamatus* | | 2 | | | | | | | | | | | | | | | | | | | |
| | *Eulalia viridis* | 4 | 8 | | | | | | | 3 | | | | | | | 1 | | | | 1 | |
| | *Phyllodoce maculata* | | | | | | | | | | | | | | | | | | | | | |
| | *Phyllodoce groenlandica* | | | | | | | | | | | | | | | | | | | | | |
| | *Nereimyra punctata* | | | | | | | | | | | | | | | | | | | | | |
| | *Kefersteinia cirrata* | | | | | | | | | | | | | | | | | | | | | |
| | *Gyptis rosea* | | 1 | | | | | | | | | | | | | | | | | | | |
| | Syllidae indet. | | | | | | | | | | | | | | | | | | | | | |
| | *Typosyllis armillaris* | 1 | 1 | | | | | | | | | | | | | | | | | | | |
| | *Exogone naidina* | | | 1 | | | | | | | | | | | | | | | | | | |
| | *Autolytus edwarsi* | | | | | | | | | | 1 | | | | | | | | | | 1 | |
| | *Platynereis dumerili* | | | | | | | | | | | | | | | | | | | | | |
| | *Nereis pelagica* | 2 | 4 | 1 | 1 | 1 | | 2 | 1 | 1 | | | | | | | 1 | | | | 1 | 1 |
| | *Nephtys* sp. | | | | | | | | | | | | | | | | | | | | | |
| | *Polydore* sp. | | | | | | | | | | | | | | | | | | | | | |
| | *Polydora ciliata* | | | | | | | | | | | | | | | | | | | | | |
| | *Arenicola marina* | | | | | | | | | | | | | | | | | | | | | |
| | Terebellidae indet. | | | | | | | | | | | | | | | | | | | | | |
| | *Nicolea zostericola* | | | | | | | | | | | | | | | | | | | | 1 | |
| | *Neoamphitrite figulus* | | 3 | | | | | | | | | | | | | | | | | | | |
| | *Polycirrus* sp. | | 1 | | | | | | | | 1 | | | | | | | | | | | |
| | Serpulidae indet. | | | | | | 1 | | | | | | | | | | | | | | | |
| | *Pomatoceros triqueter* | 2 | 5 | | 1 | | 2 | 2 | | 1 | | | | | | | | | | | | |
| | *Spirorbis* sp. | | | | | | | | | 1 | | | | | | | | | | | 1 | |

| | | Per Nilen, August, pan scourers | | | | | | | | | | Schultzs Grund, June, holdfasts | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Porifera | *Leucosolenia botryoides* | X | X | X | X | X | X | X | X | X | X | | | | | X | | | | X | X |
| | *Halisarca dujardini* | | | | | | | | X | | | | | | | | | | | | |
| | *Halichondria panicea* | | | | | | | | | | | | | | | X | | | X | | |
| Cnidaria | Scyphozoa indet. | | | | | | | | | | | 5 | | | | | | | | | |
| | Athecata indet. | | | | | | | | | | | | | | | | | | | | |
| | *Bougainvillia ramosa* | | | | | X | | | X | | | | X | | X | | X | | | | |
| | *Clava multicornis* | | | | | | | | | | | | X | X | X | X | X | X | | | X |
| | *Eudendrium arbusculum* | | | | | | | | | | | | | | | | | | | | |
| | *Opercularella lacerata* | | | | | | | | | | | X | X | | | | | | | | |
| | *Calycella syringa* | | | | | | | | | | | | | | | | | | | | |
| | *Hydrallmannia falcata* | | | | | X | | | | | | | | | | | | | | | |
| | *Sertularella rugosa* | | | | | | | | | | | | | | | | | | | | |
| | *Clytia gracilis* | | | | | | | | | | | | | | | | | | | | |
| | *Clytia hemisphaerica* | | X | | | X | X | X | X | | X | | X | | X | | | | X | | X |
| | Obeliinae indet. | | | | | | | | X | | | | | | | | | X | | X | |
| | *Gonothyraea loveni* | | | | | | | | | | | | | | | | | | | | |
| | *Obelia geniculata* | | | | | | X | X | X | | X | X | X | X | X | | X | X | | X | |
| | *Obelia longissima* | | | | | | | | | | | | | | | | | | | | X |
| | *Sagartia troglodytes* | | | | | | | | | | | | 2 | | 4 | 2 | 4 | | 2 | 5 | 3 |
| | *Sagartiogeton undatus* | | | | | | | | | | | | | | | | 7 | | | | |
| | *Metridium senile* | | | | | | | | | | | | | | | | | | | | |
| Nemertea | Nemertea indet. | | | | | | | | | | | 1 | | | 1 | 1 | 2 | 1 | | | 1 |
| Sipuncula | Sipuncula indet. | | | | | | 1 | | | | | | | | | | | | | | |
| Mollusca | *Leptochiton asellus* | | | | | | | | | | | | | | | | | | | | |
| | *Lacuna vincta* | | | | | | | | | | | 1 | | | | 1 | | | | 7 | |
| | *Littorina littorea* | | | | | | | | | | | | | | 1 | | | | | 1 | |
| | *Rissoa* sp. | 40 | 195 | 13 | 197 | 209 | 76 | 25 | 223 | 95 | 65 | 1 | | | | | | | | | |
| | *Onoba semicostata* | | | | | | | | | | | | | | | | | | | | |
| | *Bittium reticulatum* | 1 | 4 | 4 | 1 | 1 | 6 | 1 | | 1 | 1 | 5 | 16 | 5 | 13 | 31 | 25 | 18 | 12 | 28 | 6 |
| | *Buccinum undatum* | | | | | | | | | | 1 | | | | | | | | | | |
| | *Chrysallida obtusa* | | | | | | | | | | | | | | | | | | | 1 | |
| | *Brachystomia rissoides* | | | | | | | | | | | | 6 | | | 2 | 4 | 1 | | | |
| | *Diaphana minuta* | | | | 1 | 1 | | | 1 | | | | | | | | | | | | |
| | *Goniodoris nodosa* | | | | | | | | | | | | | | | | | | | | |
| | *Acanthodoris pilosa* | | | | | | | | | | | | | | | | | | | | |
| | *Onchidoris muricata* | | | | | | | 1 | | | | | | | | | | | | | |
| | *Coryphella verrucosa* | | | | | | | | | | | | | | 1 | | 2 | | | | |
| | Bivalvia indet. | | | | | | | | | | | | | | | | | | | | |
| | *Modiolus modiolus* | 2 | 5 | 2 | 2 | 13 | 2 | 9 | 15 | 4 | 3 | 26 | 55 | 13 | 43 | 53 | 43 | 70 | 21 | 85 | 27 |
| | *Musculus discors* | | | | 2 | | 1 | | | | | 14 | 20 | 9 | 20 | 47 | 14 | 14 | 19 | 42 | 27 |
| | *Anomia* sp. | | | | | | | | | | 1 | 2 | | | | 3 | 2 | | | | |
| | *Musculus* sp. | | | | | | 1 | | 1 | 1 | | | | | | | | | | | |
| | *Mysella bidentata* | | | | 1 | | | | | | | | | | 1 | 2 | 2 | 1 | 1 | | |
| | *Parvicardium* sp. | | | | | 1 | | | | | | | | | | | | | | | |
| | *Parvicardium ovale* | | | | 2 | 2 | 1 | | 6 | 1 | | | | | | | | | | | |
| | *Hiatella arctica* | 19 | 21 | 2 | 18 | 55 | 21 | 15 | 77 | 17 | 5 | 4 | 12 | 8 | 3 | 12 | 5 | 7 | 12 | 2 | 8 |
| | *Thracia phaseolina* | | | | | | | | | | | | | 1 | | 2 | | | | | |
| Annelida | *Polychaeta indet.* | | | | | | | | | | | 1 | 1 | | | | | | 1 | | |
| | *Harmothoe* sp. | | | | | | | | | | | | | | | | | | | 5 | |
| | *Harmothoe imbricata* | 7 | 8 | 7 | 10 | 12 | 10 | 8 | 12 | 7 | 8 | 4 | 4 | 2 | 9 | 10 | 2 | 2 | 3 | | 3 |
| | *Lepidonotus squamatus* | | | | 2 | | | | | | | | | | | 7 | | | | | |
| | *Eulalia viridis* | | | | | | 1 | | 1 | | | | | | | | | | | | |
| | *Phyllodoce maculata* | 2 | 2 | | | | 1 | | 1 | 1 | | | | | | | | | | | |
| | *Phyllodoce groenlandica* | | | | | | | | | | 1 | | | | | | | | | | |
| | *Nereimyra punctata* | | | | | | | | | | | | | 4 | 6 | 1 | | | | | |
| | *Kefersteinia cirrata* | | | | | | | | | | | | 4 | | 2 | | 12 | | 3 | | |
| | *Gyptis rosea* | | | | | | | | | | | 6 | | | | 1 | | 1 | 2 | | |
| | Syllidae indet. | | | | | | | | | | | | | | | 1 | | | | | |
| | *Typosyllis armillaris* | | | | | | | | | | | | | | | | | | | | |
| | *Exogone naidina* | | | 1 | | | | | 2 | | | | | | | | | | | | |
| | *Autolytus edwarsi* | 1 | | | | | | | | | | | 2 | 1 | | | | | 1 | | |
| | *Platynereis dumerili* | | 2 | | | | | | | | | | | | | | | | | | |
| | *Nereis pelagica* | 1 | | | 2 | 2 | 10 | | 2 | | 5 | 9 | 13 | 3 | 2 | 2 | 11 | 11 | 7 | 6 | 3 |
| | *Nephtys* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Polydore* sp. | | | | | | | | | | | 3 | | 4 | 1 | | | | | | |
| | *Polydora ciliata* | | | | | | | | | | | | | | | 1 | 22 | 1 | | | 2 |
| | *Arenicola marina* | | | | | | | | | | | | | 1 | | | | 1 | | | 1 |
| | Terebellidae indet. | | | | | | | | | | | | | | | | | | | | |
| | *Nicolea zostericola* | 1 | | | | | 2 | 1 | | | | | | | | | | | | | |
| | *Neoamphitrite figulus* | | | | | | | | | | | | | | | | | | | | |
| | *Polycirrus* sp. | | | | | | | | | | | | | | | | | | | | |
| | Serpulidae indet. | | | | | | | | | | | | | | | | 1 | | 2 | | |
| | *Pomatoceros triqueter* | | | | | | | | | | | 5 | | | 2 | 1 | 9 | | | | 1 |
| | *Spirorbis* sp. | | | | | | | | | | | 1 | | | 1 | | | | | | 1 |

| | | Schultzs Grund, August, holdfasts | | | | | | | | | | Schultzs Grund, August, pan scourers | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 11 |
| Porifera | *Leucosolenia botryoides* | X | X | X | | X | | X | | | X | X | | X | X | X | X | X | X | X | X |
| | *Halisarca dujardini* | | | | | | | | | | | | | | | | | | | | |
| | *Halichondria panicea* | X | X | | X | X | X | | X | X | | | | | | | | | | | |
| Cnidaria | Scyphozoa indet. | | | | 6 | | | 19 | 18 | | 13 | 53 | 2 | 19 | 20 | 4 | 1 | 30 | 3 | 13 | |
| | Athecata indet. | | | | | | | | | | | | | | | | | | | | |
| | *Bougainvillia ramosa* | | | X | | X | X | | X | X | X | X | | X | | | X | X | X | X | X |
| | *Clava multicornis* | | | | | | | | | | | X | | | X | X | | | X | | |
| | *Eudendrium arbusculum* | | X | | | | | | | | X | | | | X | | | | | | |
| | *Opercularella lacerata* | | | | | | | | | | | X | | | | | | | | | |
| | *Calycella syringa* | | | | | | | | | | | | | | | | | | | | |
| | *Hydrallmannia falcata* | | | | | | | | X | | | | | | | | | | | | |
| | *Sertularella rugosa* | | | | | | | | | | | | | | | | | | | | |
| | *Clytia gracilis* | | | | | | | | | | | | | | | | | | | | |
| | *Clytia hemisphaerica* | | | | X | X | X | X | X | X | X | X | | X | | | | X | X | X | X |
| | Obeliinae indet. | | X | | | | X | | | | | | | | | | | | | | |
| | *Gonothyraea loveni* | | | | | | | | | | | X | | | | | | | | | |
| | *Obelia geniculata* | | | X | X | X | X | X | X | X | X | X | X | X | X | | X | X | X | X | X |
| | *Obelia longissima* | | | | | | | | | | | | | | | | | | | | |
| | *Sagartia troglodytes* | 2 | 3 | | 2 | 3 | 1 | 4 | 2 | 4 | 3 | | | 1 | | | | | 1 | | 1 |
| | *Sagartiogeton undatus* | | | | | | | | | | | | | | | | | | | | |
| | *Metridium senile* | | 1 | | | | | | | | 2 | | | | | | | | | | |
| Nemertea | Nemertea indet. | | | | | | | 1 | | | | | | | | | | | | | |
| Sipuncula | Sipuncula indet. | | | | | | | | | | | | | | | | | | | | |
| Mollusca | *Leptochiton asellus* | | | | | | | | | | | | | | | | | | | | |
| | *Lacuna vincta* | 6 | | | 1 | | | 2 | | 1 | 2 | | | | 1 | 1 | | | | | 1 |
| | *Littorina littorea* | | | | | | | | | | | | 2 | | | | | | | | |
| | *Rissoa* sp. | | | | | | 1 | 1 | | 1 | | 5 | | | | | | 1 | | | |
| | *Onoba semicostata* | | | | | | | | | | | | | | | | | | | | |
| | *Bittium reticulatum* | | 1 | 8 | 1 | 2 | 4 | 1 | 1 | 3 | | 28 | 16 | 13 | 25 | 42 | 9 | 41 | 15 | 19 | 14 |
| | *Buccinum undatum* | | | | | | | | | | | | | | | | | | | | |
| | *Chrysallida obtusa* | | | | | | | | | | | | | | | | | | | | |
| | *Brachystomia rissoides* | | | | 1 | | | 1 | | | | | | | | | | | | | |
| | *Diaphana minuta* | | | | | | | | | | | | | | | | | | | | |
| | *Goniodoris nodosa* | | | | | | | | | | | | | | | | | | | | |
| | *Acanthodoris pilosa* | | | 1 | | | | | | | | | | | | | | | | | |
| | *Onchidoris muricata* | | | | | | | | | | 1 | 1 | | | | | | | | | |
| | *Coryphella verrucosa* | | | | | | | | | | | | | 1 | | 1 | | | 1 | | 1 |
| | Bivalvia indet. | | | | | | | | | | | | | | | | | | | | |
| | *Modiolus modiolus* | 5 | 3 | 5 | 8 | 12 | 16 | 17 | 9 | 9 | 15 | 70 | 9 | 62 | 39 | 12 | 8 | 34 | 108 | 28 | 46 |
| | *Musculus discors* | 8 | 9 | 3 | 10 | 3 | 21 | 20 | 2 | 8 | 8 | 1 | | 2 | 1 | 2 | 4 | 4 | 1 | | 2 |
| | *Anomia* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Musculus* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Mysella bidentata* | | | | | | | | | | | | | | | | | | | 1 | |
| | *Parvicardium* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Parvicardium ovale* | | | | | | 1 | | | | 1 | 5 | | 1 | 1 | | 2 | 1 | | 5 | |
| | *Hiatella arctica* | 6 | 3 | 5 | 11 | 7 | 23 | 19 | 5 | 8 | 19 | 71 | 8 | 22 | 8 | 10 | 6 | 27 | 30 | 16 | 15 |
| | *Thracia phaseolina* | | | | | | | | | | | | | | | | | | | | |
| Annelida | *Polychaeta indet.* | | | | | | | | | | | | | | | | | | | | |
| | *Harmothoe* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Harmothoe imbricata* | 5 | 6 | 3 | 5 | 6 | 21 | 10 | 4 | 1 | 6 | 12 | 1 | 11 | 7 | 6 | 6 | 9 | 10 | 11 | 10 |
| | *Lepidonotus squamatus* | | | | | 1 | 6 | | | | | | | | | | | | | | |
| | *Eulalia viridis* | | | | | | | 1 | | | | | | | | | | | | | |
| | *Phyllodoce maculata* | | | 1 | | | | | | | | | | | | | | | | | |
| | *Phyllodoce groenlandica* | | | | | | | | | | | | | | | | | | | | |
| | *Nereimyra punctata* | 1 | 1 | | | 2 | 9 | 1 | 1 | 1 | 1 | 1 | | | | | | | | | |
| | *Kefersteinia cirrata* | | | | | | | | | | | | | | | | | | | | |
| | *Gyptis rosea* | | | | | | | | | | | | | | | | | | | | |
| | Syllidae indet. | | | | | | | | 1 | | | | | | | | | | | | |
| | *Typosyllis armillaris* | | | | | | | | | | | | | | | | | | | | |
| | *Exogone naidina* | | | | | | | | | | | | | | | | | | | | |
| | *Autolytus edwarsi* | 3 | | | 2 | 1 | 1 | 4 | | 1 | | 1 | 1 | | | 1 | | 2 | | 1 | |
| | *Platynereis dumerili* | | | | | | | | | | | | | | | | | | | | |
| | *Nereis pelagica* | 10 | 3 | 6 | 9 | 5 | 35 | 14 | 3 | 5 | 16 | 6 | 7 | 4 | 7 | 6 | 7 | 14 | 10 | 7 | 2 |
| | *Nephtys* sp. | | | | | | | | | | | 1 | | | | | | | | | |
| | *Polydore* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Polydora ciliata* | | | | | | 1 | 1 | 1 | 1 | | | | | | | | | | | |
| | *Arenicola marina* | | | | | | | | | | | | | | | | | | | | |
| | Terebellidae indet. | | | | | | | | | | | | | | 2 | | | | | | |
| | *Nicolea zostericola* | | | | | | | | | | | | | 4 | | | | 6 | 4 | | 1 |
| | *Neoamphitrite figulus* | | | | | | | | | | | | | | | | | | | | |
| | *Polycirrus* sp. | | | | | | | | | | | | | | | | | | | | |
| | Serpulidae indet. | | | | | | | | | | | | | | | | | | | | |
| | *Pomatoceros triqueter* | 3 | 2 | | | | 1 | 2 | 1 | | 1 | | | | | | | | | | |
| | *Spirorbis* sp. | | | | | | | | | | | | | | | | | | | | |

| | | Per Nilen, June, holdfasts | | | | | | | | | | | | Per Nilen, August, holdfasts | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| | *Spirorbis tridentatus* | 8 | 38 | | 1 | | 7 | | | | | | | | | | | | | | | |
| | *Spirorbis corallinae* | | 7 | | | 19 | | 1 | | | | | | | | | | | | 1 | | |
| | Oligochaeta indet. | | | | | | | | | | | | | | | | | | | | | |
| Arthropoda | *Nymphon brevirostre* | | | | | | | | | | | | | | | | | | | | | |
| | *Callipallene brevirostris* | | | | | | | | | | | | | | | | | | | | | |
| | *Phoxichilidium femoratum* | | | | | 1 | | | | | | | | | | | | | | | | |
| | *Anoplodactylus pygmaeus* | | | | | | | | | | | | | | | | | | | | | |
| Crustacea | Thoracica indet. | 1 | 4 | | | | | 1 | 1 | | | | | | | | | | | | 2 | |
| | Amphipoda indet. | | | | | | | | | | | | | | 1 | | | | | | | |
| | Gammaridea indet. | | | | | | | | | | | | | | | | | | | | | |
| | *Gammarellus homari* | | | | | | | | | | | | | | | | | | | | | |
| | *Calliopius laeviusculus?* | | | | | | | | | | | | | | | | | | | | | |
| | *Apherusa jurinei* | | | | | | | | | | | | | | | | | | | | | |
| | *Apherusa bispinosa* | | | | | | | | | | | | | | | | | | | | | |
| | Stenothoidae indet. | | | | | | | 1 | | | | | | | | | | | | | | |
| | *Dexamine spinosa* | | | | | | | | | | | | | | | | | | | | | |
| | Ischyroceridae indet. | | | | | | | | | | | | | | | | | | | | | |
| | *Parajassa pelagica* | | | | | | | | | 1 | | | | | 1 | | | | | | | |
| | *Jassa* sp. | | | | | | | 3 | | | | | | | | | | | | | | |
| | *Ischyrocerus anguipes* | | | | | | | | | | | | | | | | | | | | | |
| | *Aora typica* | | | | | | | | | | | | | | | | | | | | | |
| | *Corophium insidiosum* | 20 | 25 | | 3 | | | 1 | 1 | 8 | 10 | | 2 | | | | | | | | | |
| | *Corophium bonelli* | 2 | 1 | | | 1 | | | | 3 | | | | | | | | | | | | |
| | *Amphithoe rubricata* | | | | | | | | | | | | | | | | | 1 | | | | |
| | *Phthisica marina* | 1 | | | | | | | | | | | | | | | | | | | | |
| | *Caprella* sp. | | 2 | | | | | 11 | | | | | | | | 1 | 1 | | | 2 | | 3 |
| | *Idotea granulosa* | | | | | | | | | | | | | | | | | | | | | |
| | Caridea indet. | | | | | | | | | | | | | | | | | | | | | |
| | *Galathea* sp. | | | | | | | | | | | | | | | | | | | | | |
| | Brachyura indet. | 2 | | | | | | | | | | | | | | | | | | | | 1 |
| Entoprocta | *Barentsia gracilis* | | | | | | | | | | | | | | | | | | | | | |
| Bryozoa | *Crisia eburnea* | X | | | X | | | | | | | | | | | | | | | | | |
| | *Filicrisia geniculata* | | | | | | | | | | | | | | | | | | | | | |
| | *Plagioecia patina* | | | | | X | X | | | X | X | | | | | | | | | | X | |
| | *Tubulipora aperta?* | | | | | | | | | | | | | | | | | | | | | |
| | *Alcyonidium hirsutum* | | | | | | | | | | | | | | | | | | | | X | |
| | *Alcyonidium gelatinosum* | | | | | | | | | | | | | | | | | | | | | |
| | *Flustrellidra hispida* | | | | | | | | | | | | | | | | | | | | | |
| | *Bowerbankia gracilis?* | | | | | | | | | | | | | | | | | | | | | |
| | *Walkeria uva?* | | | | | | | | | | | | | | | | | | | | | |
| | *Aetea truncata* | | | | | | | | | | | | | | | | | | | | | |
| | *Scruparia* sp. | | | | | | | | | | | | | | | | | | | | | |
| | *Membranipora membranacea* | X | | | X | | | | | | | | X | | | | | | X | X | | |
| | *Electra pilosa* | X | X | | X | X | X | X | X | X | | | X | X | X | X | X | | X | X | X | X |
| | *Flustra foliacea* | | | | | | | | | | | | | X | | | | | | | | |
| | *Callopora lineata* | X | X | X | X | X | | X | X | X | X | | X | X | X | | X | X | X | | X | |
| | *Amphiblestrum auritum* | | | | | | | | | | | | | | | | | | | | | |
| | *Scrupocellaria reptans* | | X | | | X | | | | | | | | | | | X | X | | | | |
| | *Scrupocellaria scabra* | | | | X | | | | | | | | | | | | | | | | | |
| | *Cribrilina cryptooecium* | | X | | | | | | | X | X | | | | | | | | | X | | |
| | *Celleporella hyalina* | X | X | X | X | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | |
| | *Cryptosula pallasiana* | | | | | | | | | X | | | | | | | X | | | X | | |
| | *Phaeostachys spinifera* | | X | | | | X | | X | X | X | | | | | | X | X | X | | X | |
| | *Escharella immersa* | X | X | | | X | X | | | X | | | | X | | | X | | | | X | X |
| Echinodermata | *Asterias rubens* | | 1 | | 1 | | | 2 | | | | | | | | 1 | | 1 | | | | |
| | *Ophiopholis aculeata* | | | | | 2 | | 1 | | | | | | | | | | | | | | |
| | *Ophiothrix fragilis* | | | | | | | | | | | | | | | | | | | | 1 | |
| | Echinoidea indet. | | | | | | | | | | | | | | | | | | | | | |
| Chordata | *Dendrodoa grossularia* | 3 | | | | | | 1 | | | | | | | | | | | | | | |
| | *Molgula* sp. | | | 2 | | | | | | | | | | | | | | | | | | |
| | *Branchiostoma lanceolatum* | | | | | | | | | | | | | | | | | | | | | |
| | Total no. of species | 25 | 28 | 9 | 14 | 17 | 13 | 22 | 11 | 18 | 12 | 3 | 11 | 8 | 11 | 5 | 12 | 9 | 11 | 11 | 17 | 11 |

| | | Per Nilen, August, pan scourers | | | | | | | | | | Schultzs Grund, June, holdfasts | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| | *Spirorbis tridentatus* | | | | | | | | | | | | | | | | | | | | |
| | *Spirorbis corallinae* | | | | | | | | | | | | | | | | | | | | |
| | Oligochaeta indet. | | | | | | | | | | | | 2 | | | 1 | | | 1 | | 1 |
| Arthropoda | *Nymphon brevirostre* | | | 1 | | | 1 | 1 | | 1 | | | | | | | | | | | |
| | *Callipallene brevirostris* | 1 | | | | | | | | 1 | | | | | 1 | | | | | 1 | |
| | *Phoxichilidium femoratum* | | | | | | | | | | | | | | | | | | | | |
| | *Anoplodactylus pygmaeus* | | | | | 1 | | | | | 1 | | | | | | | | | | |
| Crustacea | Thoracica indet. | | | | | | | | | | | | | | | | | | | | |
| | Amphipoda indet. | | | | | | | | | | | | | | | | | | | | |
| | Gammaridea indet. | 1 | 2 | | | | | | 3 | | | | 2 | | | | | | | 11 | |
| | *Gammarellus homari* | | | | | | | | | | | | | | | 1 | | | | | |
| | *Calliopius laeviusculus?* | | | | | | | | | | | | | | | | | | | | |
| | *Apherusa jurinei* | | | | | | | | | | | | | | | | | | | | |
| | *Apherusa bispinosa* | 45 | 18 | 23 | 7 | 34 | 43 | 10 | 8 | 15 | 19 | | | | | | | | | | |
| | Stenothoidae indet. | | | | | 1 | | | | 2 | | | 7 | | | | | | 1 | | |
| | *Dexamine spinosa* | 3 | 2 | | 7 | 3 | 4 | 8 | 5 | 3 | 9 | | | | | | | | | | |
| | Ischyroceridae indet. | | | | | 4 | | | | | | | | | | | | | | | |
| | *Parajassa pelagica* | | | | | 1 | | 1 | | | 1 | | | | | | | | | | |
| | *Jassa* sp. | 1 | | | | | | | | | | | 5 | | | | | | | | |
| | *Ischyrocerus anguipes* | | | | | | | | | | | | | | | | | | | 5 | |
| | *Aora typica* | 3 | 3 | 1 | | | | | | | | | | | | | | | | | |
| | *Corophium insidiosum* | 3 | 18 | 3 | 3 | 10 | 34 | 2 | 9 | 21 | 10 | | | | 2 | 3 | | 1 | | 1 | |
| | *Corophium bonelli* | 11 | 24 | 5 | 5 | 11 | 53 | | 17 | 23 | 5 | | | | 1 | 2 | | | | 1 | |
| | *Amphithoe rubricata* | 8 | 16 | 42 | 13 | 21 | 76 | 8 | 16 | 11 | 11 | | | | | 2 | 1 | 1 | | 16 | 1 |
| | *Phthisica marina* | 4 | 1 | | 1 | | | | 2 | 1 | | | | | | | | | | | |
| | *Caprella* sp. | 4 | 2 | | 2 | 6 | | 1 | 2 | 1 | 2 | | 10 | 2 | | | 1 | | | 2 | |
| | *Idotea granulosa* | | | | | | | | | | | | 2 | | | 3 | | | | 20 | |
| | Caridea indet. | 1 | | | 1 | | | | 1 | | | | | | | | | | | | |
| | *Galathea* sp. | | | | | | 4 | | | | | | | | | | | | | | |
| | Brachyura indet. | 5 | 4 | 2 | | 1 | 3 | 2 | | 1 | | | | | | | | | | | |
| Entoprocta | *Barentsia gracilis* | | | | | | | | | | | | | | | | | | | | |
| Bryozoa | *Crisia eburnea* | X | X | X | X | X | X | X | X | X | X | | | | | X | | | | | |
| | *Filicrisia geniculata* | | | | | | | | | X | | | | | | | | | | | |
| | *Plagioecia patina* | | | | | | | | | | X | | | | | | | | | | |
| | *Tubulipora aperta?* | | | | | X | | X | | | | | | | | | | | | | |
| | *Alcyonidium hirsutum* | | | | | X | | | X | | | | | | | | | | | | |
| | *Alcyonidium gelatinosum* | | | | | X | | | | | | | | | | X | X | X | | | X |
| | *Flustrellidra hispida* | | | | | | | | X | | | | | | | | | | | | |
| | *Bowerbankia gracilis?* | | | | | | | | | | | | | | | X | | | | | X |
| | *Walkeria uva?* | | | | | X | | X | X | | | | | | | X | | | X | | X |
| | *Aetea truncata* | | | | | X | | X | X | X | | | | | | | | | | | |
| | *Scruparia* sp. | | | | | X | | | X | | | | | | | | | | | | |
| | *Membranipora membranacea* | X | X | | | X | | X | X | | X | | X | | | | | | | | |
| | *Electra pilosa* | X | X | | | X | X | X | X | X | X | X | X | X | X | X | | | X | X | X |
| | *Flustra foliacea* | | | | | | | | | | | | | | | | | | | | |
| | *Callopora lineata* | | X | X | | X | X | X | X | X | X | | | | | | | | | | |
| | *Amphiblestrum auritum* | | | | | | | | | | | X | X | X | X | X | X | X | X | X | X |
| | *Scrupocellaria reptans* | X | X | | | X | | X | X | X | | | | | | | | | | | |
| | *Scrupocellaria scabra* | | | | | | | | | | | | | | | | | | | | |
| | *Cribrilina cryptooecium* | | | | | | | | | | | X | | | | | | | | | |
| | *Celleporella hyalina* | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | |
| | *Cryptosula pallasiana* | | | | | | | | | | | | | | | | | | | | |
| | *Phaeostachys spinifera* | | | | | | | | | | | | | | | | | | | | |
| | *Escharella immersa* | | | | X | | | | | | | | | | X | | | | | | |
| Echinodermata | *Asterias rubens* | 4 | 3 | 12 | | 3 | 5 | 9 | 3 | 5 | 11 | | 1 | 2 | 2 | 3 | 5 | 1 | | 2 | |
| | *Ophiopholis aculeata* | | | | | | | | | | | | | | | | | | | | |
| | *Ophiothrix fragilis* | | 1 | 1 | | 1 | 1 | 1 | 1 | | | 1 | | | | | | | | | |
| | Echinoidea indet. | | | | 1 | 2 | | | | 1 | 2 | 1 | | | | | | | | | |
| Chordata | *Dendrodoa grossularia* | | | | | | | | | | | | | | | | | | | | |
| | *Molgula* sp. | | | | | | | | | | | | | | 5 | | | | | | |
| | *Branchiostoma lanceolatum* | | | | | 1 | | | | | | | | | | | | | | | |
| | Total no. of species | 29 | 27 | 19 | 24 | 40 | 30 | 29 | 39 | 29 | 28 | 23 | 26 | 17 | 28 | 35 | 25 | 20 | 20 | 24 | 23 |

| | | Schultzs Grund, August, holdfasts | | | | | | | | | | Schultzs Grund, August, pan scourers | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phylum | Species/taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 11 |
| | *Spirorbis tridentatus* | | | | | | | | | | | | | | | | | | | | |
| | *Spirorbis corallinae* | | | | | | | | | | | | | | | | | | | | |
| | Oligochaeta indet. | | | 1 | | | | | | | | | | | | | | | | | |
| Arthropoda | *Nymphon brevirostre* | 2 | 4 | | | 1 | | | | | 2 | | | 5 | | 2 | 1 | 1 | 5 | 1 | |
| | *Callipallene brevirostris* | 2 | 2 | | 1 | 3 | 5 | 1 | 1 | | 4 | 5 | 2 | 3 | 4 | 1 | | | 3 | 8 | 3 |
| | *Phoxichilidium femoratum* | | | | | | | | | | | | | | 1 | | | | | | |
| | *Anoplodactylus pygmaeus* | | | | | | | | | | | | | | | | | | | | |
| Crustacea | Thoracica indet. | | | | 2 | | 1 | | | | | | | | | | | | | | |
| | Amphipoda indet. | | | | | | | | | | | | | | | | | | | | |
| | Gammaridea indet. | | | | | 1 | | | | | | | | | | 1 | | 1 | | | |
| | *Gammarellus homari* | | | | | | | | | | | 1 | | | | | | | | | |
| | *Calliopius laeviusculus?* | | | | | | | | | | | 1 | | | | | | | | | |
| | *Apherusa jurinei* | 3 | | | | | | | | | | | | | | | | | | | |
| | *Apherusa bispinosa* | 2 | | | | | 1 | | | | | 1 | | | 2 | | | 1 | | 1 | 1 |
| | Stenothoidae indet. | | | | | 1 | 9 | | | | | | | | | | | 1 | | | |
| | *Dexamine spinosa* | 1 | | | | | | | | | | 1 | 1 | 6 | 3 | 3 | | 1 | 5 | 3 | 3 |
| | Ischyroceridae indet. | | | | | | | | | | | | | | | | | | | | |
| | *Parajassa pelagica* | | | | | | | | | | | | | | | | | | | | |
| | *Jassa* sp. | | | | | | 3 | | | | | | | | | | | | | | |
| | *Ischyrocerus anguipes* | | | | | | | | | | | | | | | | | | | | |
| | *Aora typica* | | | | | | | | | | | | | | | | | | | | |
| | *Corophium insidiosum* | 1 | | | | 2 | 2 | | 1 | | 1 | 7 | 1 | 12 | 4 | 1 | 1 | 8 | 21 | 2 | 8 |
| | *Corophium bonelli* | | | | | | | | | | | | | 1 | 1 | | | | | | |
| | *Amphithoe rubricata* | 19 | 3 | 9 | 3 | 4 | 23 | | 7 | 1 | 17 | 7 | | 24 | 9 | 5 | 3 | 34 | 58 | 3 | 7 |
| | *Phthisica marina* | | | | | | | | | | | | | | | | | | | | |
| | *Caprella* sp. | 16 | | 2 | | | 16 | | 1 | | 1 | 1 | 1 | | 1 | 2 | 1 | 2 | 1 | 2 | 2 |
| | *Idotea granulosa* | 2 | 1 | 3 | 1 | | 2 | | | | | | | | | | | 1 | | | 1 |
| | Caridea indet. | | | | | | | | | | | | | | | | | | | | |
| | *Galathea* sp. | | | | | | | | | | | | | | | | | | | | |
| | Brachyura indet. | | | | | | | | | | | | | | | 1 | | 1 | | | |
| Entoprocta | *Barentsia gracilis* | | | | | | | | X | | | | | | | | | | | | |
| Bryozoa | *Crisia eburnea* | | | | | | | | | | | | | | | | | | | | |
| | *Filicrisia geniculata* | | | | | | | | | | | | | | | | | | | | |
| | *Plagioecia patina* | | | | | | | | | | | | | | | | | | | | |
| | *Tubulipora aperta?* | | | | | | | | | | | | | | | | | | | | |
| | *Alcyonidium hirsutum* | | | | | | | | | | | | | | | | | | | | |
| | *Alcyonidium gelatinosum* | X | | X | X | X | X | X | X | X | X | | | | | | | | | | |
| | *Flustrellidra hispida* | | | | | | | | | | | | | | | | | | | | |
| | *Bowerbankia gracilis?* | | X | | | | | | | | | | | | | | | | | | |
| | *Walkeria uva?* | | | X | | | | | | | | | | | X | | | | | | |
| | *Aetea truncata* | | | | | | | | | | | | | | | | | | | | |
| | *Scruparia* sp. | | | | | | | | | | | | | | | | | | | | |
| | *Membranipora membranacea* | | | | X | | | | | | | X | | | | | | | | X | |
| | *Electra pilosa* | X | X | X | X | X | X | | X | | X | X | X | X | X | X | X | X | X | X | X |
| | *Flustra foliacea* | | | | | | | | | | | | | | | | | | | | |
| | *Callopora lineata* | | | | | | | | | | | | | | | | | | X | | |
| | *Amphiblestrum auritum* | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | |
| | *Scrupocellaria reptans* | | | | | | | | | | | | | | | | | | | | |
| | *Scrupocellaria scabra* | | | | | | | | | | | | | | | | | | | | |
| | *Cribrilina cryptooecium* | | | | | | | | | | | | | | | | | | | | |
| | *Celleporella hyalina* | | | | | | | | | | | | | | | | | | | | |
| | *Cryptosula pallasiana* | | | | | | | | | | | | | | | | | | | | |
| | *Phaeostachys spinifera* | | | | | | | | | | | | | | | | | | | | |
| | *Escharella immersa* | | | | | | | | | | | | | | | | | | | | |
| Echinodermata | *Asterias rubens* | | | 1 | 2 | 1 | 10 | 6 | 3 | | 3 | 25 | 11 | 22 | 14 | 11 | 17 | 21 | 17 | 23 | 17 |
| | *Ophiopholis aculeata* | | | | | | | | | | | | | | | | | | | | |
| | *Ophiothrix fragilis* | | | | | | | | | | | | | | | | | | | | |
| | Echinoidea indet. | | | | | | | | | | | | | | | | | | | | |
| Chordata | *Dendrodoa grossularia* | | | | | | | | | | | | | | | | | | | | |
| | *Molgula* sp. | | | 1 | | | 3 | | | | | | | | | | | | | | |
| | *Branchiostoma lanceolatum* | | | | | | | | | | | | | | | | | | | | |
| | Total no. of species | 24 | 21 | 21 | 23 | 25 | 33 | 24 | 26 | 19 | 27 | 31 | 15 | 23 | 25 | 22 | 17 | 27 | 24 | 23 | 23 |

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