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Alcyonidium disciforme: an exceptional Arctic bryozoan

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The ctenostome bryozoan *Alcyonidium disciforme* is the only known free-living Arctic bryozoan. *Alcyonidium disciforme* has a strictly Arctic circumpolar distribution. The material studied was collected during 1995–2002 in West Spitsbergen, Svalbard. Densities of the bryozoan in Van Veen grab and SCUBA diving samples are presented together with environmental data. *Alcyonidium disciforme* is restricted to the inner part of Kongsfjorden—main area of study. The activity of the tidal glacier situated in the inner part of the fjord results in strong environmental gradients, meltwater outflows causing salinity and temperature fluctuations together with high concentrations and rates of mineral material sedimentation. The wide bathymetric range of the species (8 to 240 m) suggests that depth is not its limiting factor within the fjord. High densities of *A. disciforme* recorded in shallow glacial bay waters indicate that it is highly tolerant of fluctuations in salinity. It also tolerates high mineral sedimentation rates; this is unusual for a suspension-feeding animal. The species has a very regular disc-like shape. Colonies develop a central hole when they reach approximately 3 mm in diameter. There are significant positive correlations between wet mass vs colony diameter, wet mass vs central hole diameter, and diameter of the whole colony vs central hole diameter. *Alcyonidium disciforme* is adapted, through its colony shape and zooids filled with sand particles acting as a ballast to survive in a dynamic sedimentary environment.

INTRODUCTION

Alcyonidium disciforme Smitt, 1871 is a ctenostome bryozoan. The type specimen was collected during the Smitt expedition to Spitsbergen in 1868, on-board the iron-steamer 'Sofia', led by the Swedish geologist Nordenskiold (Smitt, 1871; Nathorst et al., 1909).

An Arctic, circumpolar species (for a more detailed distribution see Figure 1), the most southerly record (60°N) of *A. disciforme* is from Wakeham Bay in Canada (Osburn, 1953), while the most northerly record is the Jørgen Brønlund Fjord (82°N) in northern Greenland (Andersen, 1973). Ecological and biological knowledge is scant. Most of the ecological data regarding *A. disciforme* was published by Russian researchers (Kluge, 1975; Androsova, 1977; Denisenko, 1990). Androsova (1977) presented the first quantitative description of a species population. Her data from Franz Josef Land revealed that *A. disciforme* density reached over 45 colonies and 36 grams of biomass per square metre. In terms of biomass this makes the species an important contributor to the biomass of Arctic benthic communities, which was reported to vary from 4 to 643 g of wet mass/m^2 (Carey, 1991; Włodarska-Kowalczuk et al., 1998).

Why is *A. disciforme* exceptional? It is the only free-living, non-attached, bryozoan known from the Arctic (Kluge, 1975). There are other examples of free-living bryozoans (lunulitiforms), but their occurrence is restricted to warm waters (Cook & Chimonides, 1994). The shape of the colony is also unusual (Figure 2). Mature colonies have a ring-like appearance, with an opening in the middle of the colony. Kluge (1975), in his monograph on Arctic bryozoans, presented the first observations on colony development. Initially, the colony has the appearance of a more or less convex disc. As growth continues (5–6 mm in diameter) a round hole appears in the middle of the colony, giving the colony a ring-like appearance (Kluge, 1975). The oldest colony recorded in the literature was 5–6 y old (Kluge, 1975). Kvitek (1989) found that the shape of the colony is an adaptation to the highly dynamic sedimentary habitat. *Alcyonidium disciforme* occurs in unstable, soft sediments—an environment unusual for bryozoans and for suspension feeders in general.

In Svalbard waters the species has been recorded only in glacial bays (Kirkpatrick, 1925; Włodarska et al., 1996; Gontar et al., 2001; Kukliński, 2002; J.M. Węsławski, unpublished data; present observations). Glacial meltwater outflows result in salinity and temperature fluctuations, and high concentrations and high rates of mineral material sedimentation (Elverhøi et al., 1983; Svendsen et al., 2002). The activity of tidal glaciers situated in the inner part of the fjords results in strong environmental gradients (Syvitski et al., 1987; Svendsen et al., 2002) which influence both pelagic and benthic biota (Włodarska-Kowalczuk et al., 1998; Syvitski et al., 1987).

The species is an important component of the benthos of Arctic glacial bays, and has potential as a bioindicator of specific hydrographic conditions. With the ongoing coastal change and massive glacial melt in the Arctic, *A. disciforme* may become widespread as a result of such changes in hydrographic conditions.

The aim of the present study is to provide a detailed description of the species' distribution in relation to

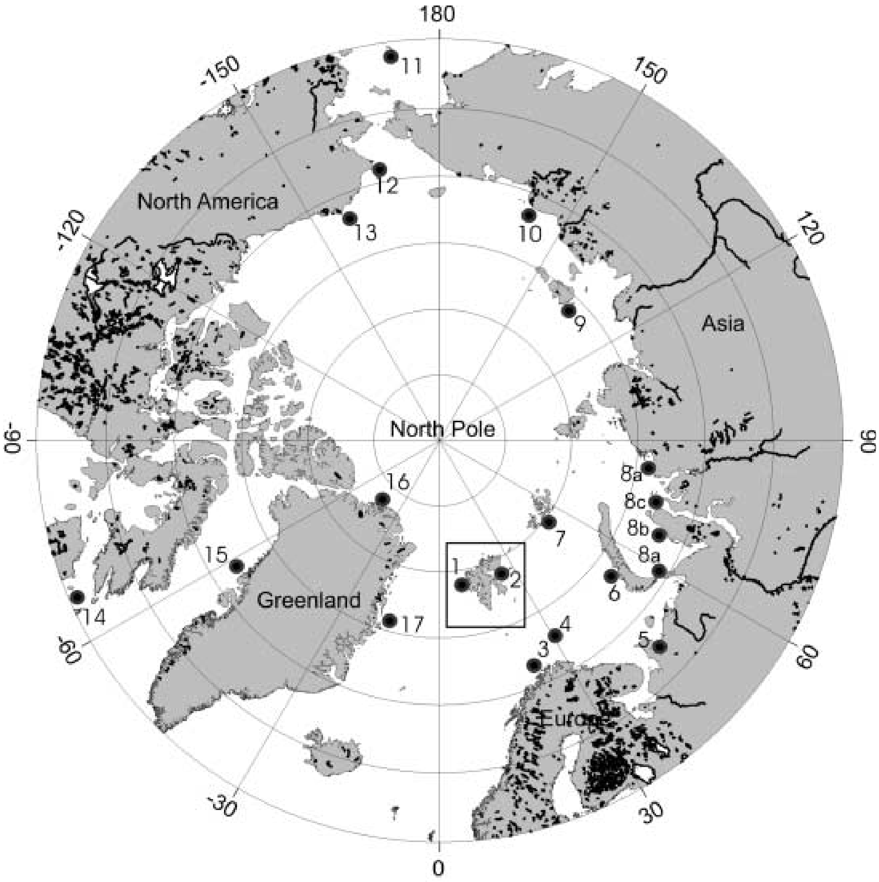

Figure 1. Global distribution of *Alcyonidium disciforme*—in the frame area of study (**1.** West Spitsbergen—Smitt, 1871; Kirkpatrick, 1925; Włodarska et al., 1996; Gontar et al., 2001; Kukliński 2002; **2.** East Spitsbergen—Bidenkap, 1897, 1900; **3.** northern Norway—Bidenkap, 1905; Nordgaard, 1905, 1912a, 1918; **4.** Barents Sea—Nordgaard, 1900; Calvet, 1903; Denisenko, 1990; **5.** Pechora Sea—Pogrebov et al., 1997; Dahle et al., 1998; **6.** Novaya Zemlya—Stuxberg, 1887; Nordgaard, 1912b, 1923; **7.** Franz Joseph Land—Androsova, 1977; Włodarska et al., 1996; **8.** Kara Sea: **8a**—Stuxberg, 1882; **8b**—Smitt, 1879; Levinsen, 1886; **8c**—Jorgensen et al., 1999; **9.** Laptiev Sea—Abrikosov, 1932; **10.** East Siberian Sea—Kluge, 1975; **11.** Bering Sea—Kvitek, 1989; **12.** Chukchi Sea—Kvitek, 1989; **13.** Beaufort Sea—Osburn, 1953; **14.** Ungava Bay, Canada—Osburn, 1953; **15.** west of Greenland—Levinsen, 1914; **16.** northern Greenland—Andersen, 1973; **17.** east of Greenland—Andersson, 1902; Levinsen, 1914).

Figure 2. *Alcyonidium disciforme in situ*—Kongsfjorden (photo: B. Gulliksen).

environmental factors in an Arctic glacier-influenced fjord, together with some aspects of its biology, including morphometric data, morphological adaptation and histological analyses.

MATERIALS AND METHODS

Study site

The material was collected in Kongsfjorden (Figure 3), a fjord on the western coast of Spitsbergen at 79°N and 12°E. The length of coastline in the fjord is 89.6 km, 15.9 km of which is covered by glaciers. The principle factors responsible for hydrological conditions in the fjord are bathymetry, vicinity of the ocean, glaciers (presence of the four tidewater glaciers) and climate (Węsławski et al., 1991; Svendsen et al., 2002).

The area is highly influenced by Atlantic water, which enters the fjord with the inflow of the West Spitsbergen Current as Transformed Atlantic Water ($T > 1$°C, $S > 34.7$ psu) (Węsławski et al., 1991; Svendsen et al., 2002). The glacial meltwater outflow results in formation of surface water with temperature less than -0.5°C and salinity below 34.4 psu (Svendsen et al., 2002).

The inner fjord is characterized by winter (mid-December to between April and July) coverage of fast-ice (frozen sea surface) and is subject to ice scour down to 40 m depth from icebergs during summer months

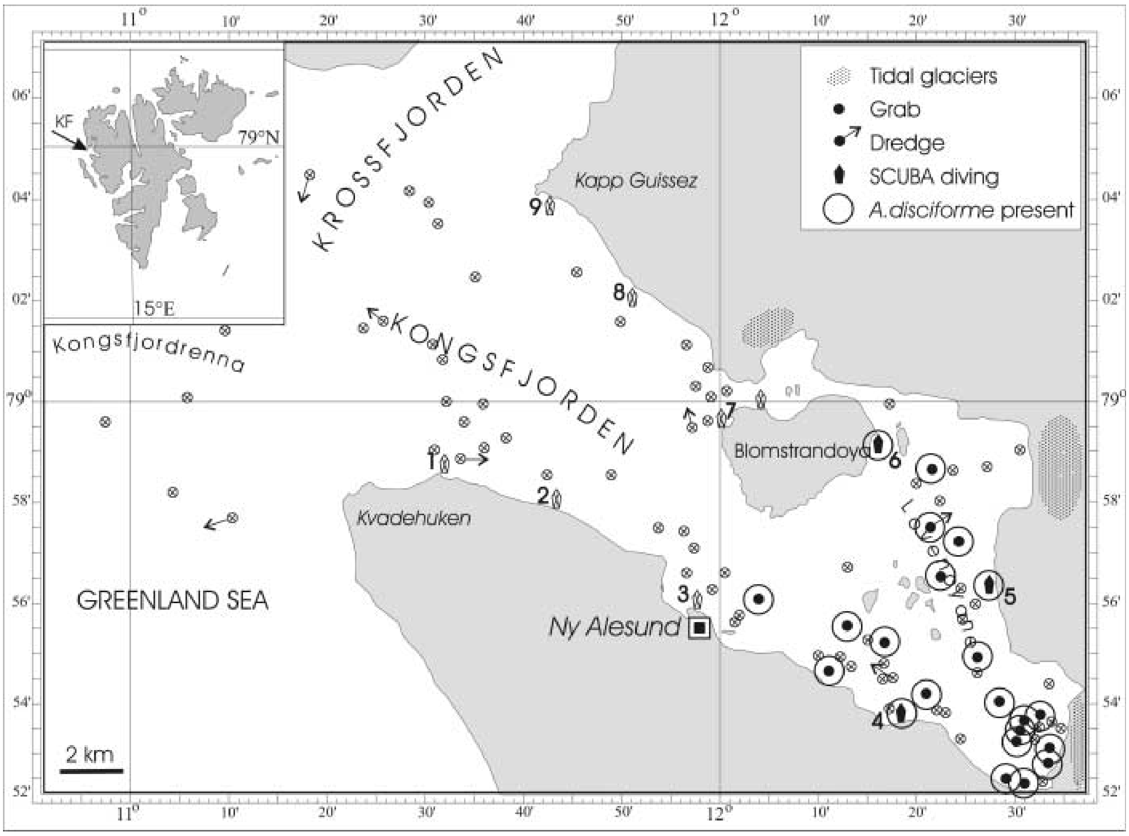

Figure 3. Distribution of *Alcyonidium disciforme* within the Kongsfjorden (number denotes the station where environmental factors were measured; KF, Kongsfjorden).

(Dowdeswell & Forsberg, 1992; Svendsen et al., 2002). The central and outer parts of the fjord are only occasionally covered with fast-ice (Svendsen et al., 2002).

Suspension concentrations in the surface plume close to glaciers can reach 300–500 mg/dm^3, decreasing in the central and outer parts of the fjord in summer. In the inner basin concentrations in the intermediate water layer may reach 20–25 mg/dm^3, in the central parts 2–3 mg/dm^3, while relatively clear water in the outer parts of the fjord contains 0.5 mg/dm^3 (Elverhøi et al., 1983; Svendsen et al., 2002). The floor of the inner basin is covered with soft sediments, while in the outer part the bottom types are much more diverse—ranging from mud, to gravel and rocky shelves (Svendsen et al., 2002).

For a more detailed study of the biological ecosystem of Kongsfjorden, see Hop et al. (2002); recent physical data for the area are presented and discussed by Svendsen et al. (2002).

Sampling programme

Samples were taken during the 1995, 1996, 1997 and 1998 cruises of RV 'Oceania', the 2001 land based project, and the 2001 and 2002 cruises of RV 'Jan Mayen'. Several techniques were used to collect the samples: a Van Veen grab (0.1 m^2), SCUBA (frame 0.25 m^2 and, on soft bottoms, cores 185 mm in diameter) and dredging. The sampling stations are illustrated in Figure 3. At each station three replicates of faunal samples were taken and the depth was recorded.

The frequency of occurrence of *Alcyonidium disciforme* was calculated, where:

$$F = n_{\mathrm{i}} * \mathrm{N}^{-1} * 100 \qquad (1)$$

F=frequency of given taxon [%]; n_{i}=number of samples where given taxon was present; N=total number of samples.

Physical factors

To confirm gradient of sedimentation rate along the fjord observed in similar systems elsewhere (Syvitski, 1987), sedimentation rate at the seabed was measured in 2001. Stations sampled included both the inner and outer parts of the fjord (see Figure 3). Tube shaped traps, 8 cm diameter and 54 cm high, were placed by divers onto the seabed and these traps were subsequently exposed for 24 hours. To minimize the effect of sediment resuspension, opening of the traps was postponed until the suspension was stabilized. At each station three replicates were taken. After a 24 h period of exposure the traps were recovered, taken to the laboratory and left for another 24 h to settle. Then, the upper 2 litres of supernatant were removed, while the remaining mixture of water and sediment was filtered through the glass fibre filters (Whatman GF/C, 47 mm). The filters were weighed before and after filtering.

In order to measure the organic content of the sediment, the GFC filters loaded with sediment were weighed, then placed in an oven (450°C) for 24 h and subsequently reweighed.

To analyse the grain size composition of the sediment, subsamples were taken from cores that had been collected by a diver. Sediment fractions were categorized as clay (<4 μm), silt (4–63 μm), sand (63–2000 μm), pebbles (2–64 mm) and cobbles (64–256 mm). Grain size measurements were made using a combination of the hydro-meter method and sieving. Subsequently all sediments were suspended in a solution of hexa-metaphosphate (5 g/l), which has the effect of reducing the links between clay particles due to flocculation. The density variation of the solution was measured at different time intervals and, finally, Stokes' law was used to compute the mean diameter of the sediment particles from their settling speed and the changing density of the solution with time. This method is described in detail by, for example, Gee & Bauder (1979). Randomly selected pebbles and cobbles were measured using callipers, and mean, standard deviation and range calculated.

Temperature and salinity measurements were conducted by the Hydrology Department (IO PAS) for the whole fjord.

Morphological studies

The collected material was fixed in 4% formaldehyde, and following sorting was transferred into 70% ethanol. All the individuals sampled in 2001 and 2002 were weighed (wet mass). Measurements of total and central hole diameter were made for all colonies using an eyepiece micrometer in a stereomicroscope.

Six specimens of *A. disciforme* from Station 5 were deposited in the Natural History Museum, London (NHM) under the registration numbers 2003.1.13.1–6. These six specimens varied in diameter (2 cm, 2.5 cm, 3.5 cm, 3.7 cm, 3.8 cm and 4.0 cm respectively) and were chosen to represent different stages of ontogeny. Histological sections were prepared from these specimens. In preparing paraffin wax sections, two pieces of tissue approximately 1×1 cm were cut from each specimen, one was embedded to be cut longitudinally and the other embedded to be cut transversely. The tissue pieces were first dehydrated through a series of ethanol: 90% overnight, followed by three changes of 100% ethanol (one every two hours); the samples were then put into a 1% Neceloidine solution for 24 h followed by chloroform for 24 hours. Finally, the samples were embedded after three changes of paraffin wax. Blocks were sectioned at 7 μm, mounted using a solution of five drops of glycerine albumin in 100 ml of distilled water, and dried on a hot plate before staining with Mallory's triple stain, using the following protocol: Histoclear 5 min, 100% ethanol 1 min, 90% ethanol 1 min, 70% ethanol 1 min, distilled water 1 min, Mallory's stain 5 min, rinse in running water for 30 s, 70% ethanol 1 min, 90% ethanol 1 min, 100% ethanol 1 min, Histoclear 5 min. Slides were mounted in DPX mountant.

Measurements were made from the cut sections of the six chosen specimens, including autozooid width and length, and diameter of developing oocytes, using an Image Analysis system (a Hitachi JVC TK1270 camera mounted on an Olympus BH2 microscope and connected to a computer). Measurements were generated with

Table 1. *Environmental data collected during the expedition in 2001—station number refers to the station presented in Figure 3.*

Station no.	1	2	3	4 ●	5 ●	6 ●	7	8	9
Environmental factors									
Latitude	78°58.5′N	78°57.3′N	78°55.8′N	78°53.5′N	78°56.5′N	78°58.9′N	78°59.5′N	79°01.8′N	79°03.5′N
Longitude	11°29.8′E	11°46.1′E	11°54.9′E	12°15.0′E	12°25.9′E	12°13.3′E	11°58.9′E	11°49.8′E	11°39.4′E
Total sedimentation g/m^2/24 h	4.62 ±0.74	11.31 ±1.78	49.47 ±8.31	58.38 ±9.73	119.78 ±5.88	59.35 ±5.1	9.11 ±1.67	91.1 ±8.25	14.03 ±0.81
Mineral sedimentation g/m^2/24 h	3.6 ±0.53	9.04 ±1.89	40.5 ±10.95	51.92 ±10.24	110.3 ±3.07	49.56 ±7.96	7.44 ±1.33	82.41 ±7.24	12.33 ±0.43
Organic sedimentation g/m^2/24 h	0.77 ±0.61	2.26 ±0.52	8.97 ±3.24	6.46 ±0.51	9.47 ±2.81	9.89 ±3.15	1.67 ±0.41	8.69 ±0.84	1.7 ±0.38
Distance from the nearest tidal glacier (km)	24.63	20.37	14.63	6.48	5.74	4.63	6.67	9.91	14.96
Clay (%)	—	—	26.61	28.98	36.08	54.87	—	—	—
Mud (%)	—	4.43	50.28	66.09	29.69	27.00	2.27	4.32	—
Sand (%)	—	23.23	10.73	4.93	29.75	9.90	5.21	35.29	7.27
Gravel (%)	100.00	72.34	12.38	—	4.48	8.91	92.52	60.39	92.73
Pebbles*	19.2 ±14.5 (2.0–63.0) N=82	9.1 ±7.2 (2.0–55.0) N=247	4.1 N=1	—	—	—	21.9 ±15.1 (2.0–63.1) N=240	17.0 ±13.3 (2.0–63.0) N=260	23.0 ±14.5 (2.0–62.0) N=82
Cobbles*	87.5 ±23.4 (65.0–139.0) N=9	—	117.6 ±31.2 (64.3–144.0) N=5	—	—	—	75.3 ±11.7 (66.0–102.0) N=12	79.4 ±3.3 (77.0–81.7) N=2	94.0 ±28.3 (65.0–156.0) N=12
Presence of bear rock	YES	NO	NO	NO	NO	NO	YES	NO	YES
Temperature (°C)	4.88	4.55	4.10	3.14	1.71	3.10	2.50	4.99	4.62
Salinity (psu)	34.02	34.17	34.35	33.23	32.90	33.27	33.43	33.66	33.77

●, *Alcyonidium disciforme* present; *, mean diameter ±SD (mm), range (mm); N, number of stones measured.

Table 2. *Correlations between environmental factors and presence of* Alcyonidium disciforme *(data taken from Table 1).*

Environmental factors	*r*	*P*
Clay	0.90	0.001
Mud	0.64	0.062
Total sedimentation	0.64	0.064
Mineral sedimentation	0.64	0.064
Organic sedimentation	0.64	0.064
Sand	0.00	1.000
Presence of bare rock	−0.50	0.170
Temperature	−0.64	0.064
Distance from nearest tidal glacier	−0.82	0.007
Gravel	−0.82	0.007
Salinity	−0.82	0.007
Cobbles	−0.84	0.005
Pebbles	−0.84	0.005

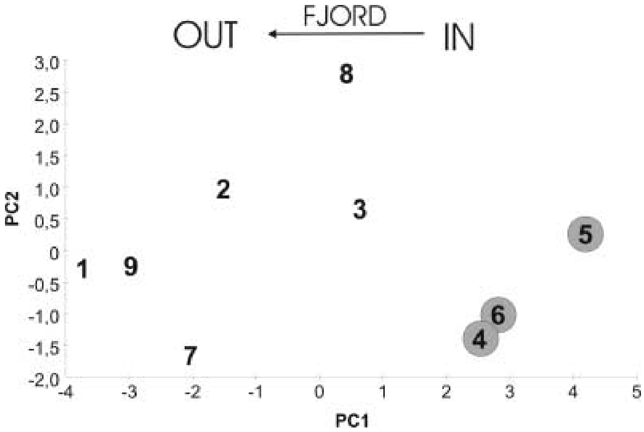

Figure 4. Principal component analyses based on data from Table 1 (stations encircled indicate presence of *Alcyonidium disciforme*).

Imagepro software, saved into an Excel datasheet and basic statistics performed.

Data analyses

To investigate the environmental factors that might be responsible for the distribution of *A. disciforme*, the PRIMER software package was used (Clarke & Warwick, 1994). An environmental data matrix was constructed and used in principal components analyses (PCA). A Draftsman plot was then produced and used to estimate correlations between each of the environmental factors.

Nonparametric Spearman correlation was used to evaluate all relationships and significance between the presence of *A. disciforme* and individual environmental factors.

Other correlations (wet mass–colony diameter; number of individuals–depth distribution; organic, mineral vs total amount of sedimentation) were tested using the parametric Pearson product–moment correlation.

Table 3. *Details of stations where* Alcyonidium disciforme *was recorded.*

No.	Date of collection (year, month, day)	Station coordinates	Gear type (no. of replicates)	Depth (m)	Individuals/m^2 (mean ±SD)	Biomass (g/m^2) (mean ±SD)
1	1995.07.22	12°26.8′E 78°54.8′N	g (3)	69	3.3 ±5.77	n.a.
2	1995.07.22	12°22.5′E 78°56.5′N	g (3)	40	3.3 ±5.78	n.a.
3	1996.07.11	12°28.6′E 78°52.5′N	g (3)	45	26.7 ±46.19	n.a.
4	1996.07.11	12°31.0′E 78°52.4′N	g (3)	15	23.3 ±40.41	n.a.
5	1996.07.11	12°33.4′E 78°52.3′N	g (3)	85	3.3 ±5.77	n.a.
6	1996.07.11	12°33.3′E 78°53.2′N	g (3)	83	3.3 ±5.77	n.a.
7	1996.07.11	12°33.1′E 78°53.9′N	g (3)	81	10.0 ±17.32	n.a.
8	1996.07.11	12°30.9′E 78°53.5′N	g (3)	88	6.7 ±11.55	n.a.
9	1996.07.11	12°31.0′E 78°53.7′N	g (3)	97	3.3 ±5.77	n.a.
10	1996.07.11	12°31.4′E 78°53.8′N	g (3)	85	3.3 ±5.77	n.a.
11	1996.07.12	12°16.2′E 78°55.2′N	d	111	52*	n.a.
12	1996.07.12	12°13.1′E 78°55.4′N	d	75	1*	n.a.
13	1996.07.12	12°10.1′E 78°54.8′N	d	70	3*	n.a.
14	1996.07.12	12°03.5′E 78°56.1′N	d	240	2*	n.a.
15	1997.07.25	12°27.9′E 78°54.0′N	g (3)	60	3.3 ±5.79	1.4 ±2.42
16	1997.07.25	12°10.9′E 78°54.1′N	g (3)	38	6.6 ±11.55	n.a.
17	1997.07.25	12°21.1′E 78°57.5N	d	80	56*	n.a.
18	1997.07.20	12°13.8′E 78°58.7′N	g (3)	70	3.3 ±5.77	n.a.
19	1998.07.10	12°24.3′E 78°57.4′N	g (3)	40	6.6 ±5.77	0.1 ±0.12
20	2001.08.07	12°25.9′E 78°56.9′N	S-c (3)	10	37.2 ±64.47	0.9 ±1.56
21	2001.08.08	12°15.0′E 78°53.5′N	S-c (3)	10	1240.6 ±1202.81	27.4 ±10.64
22	2001.08.09	12°25.9′E 78°56.9′N	S-f (3)	8	9.3 ±6.11	14.4 ±10.24
23	2001.08.13	12°13.3′E 78°58.9′N	S-f (3)	10	6.6 ±2.31	6.9 ±1.79
24	2001.08.15	12°15.0′E 78°53.5′N	S-f (3)	10	40.0 ±16.00	31.5 ±18.80
25	2001.08.14	12°15.0′E 78°53.5′N	S-f (3)	9	33.3 ±30.02	29.1 ±24.21
26	2002.09.23	12°15.0′E 78°53.5′N	S-c (5)	10	3.6 ±2.07	0.35 ±0.31

g, grab; d, dredge; S-c, core taken by SCUBA diver; S-f, sample with use of frame taken by SCUBA diver; *, no quantitative sample; n.a., not available.

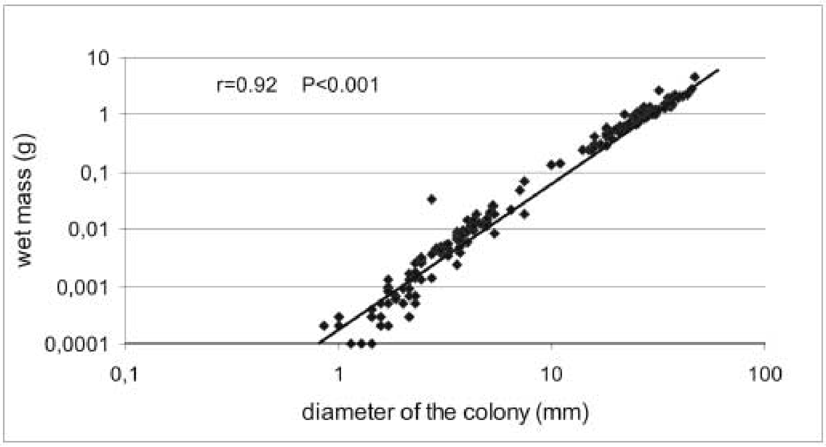

Figure 5. Relationship between wet mass and diameter of the colony.

All the statistical analyses were performed using the STATISTICA software package.

RESULTS

Sediment input to the bottom showed a gradual change, decreasing from the inner part of the fjord to the outer part except for Station 8 (Table 1). The highest value was measured at Station 5, the lowest at Station 1. The organic and mineral content of the suspended matter correlated positively with the total amount of sedimentation ($r=0.86$; $P<0.05$; $r=0.99$, $P<0.05$ respectively).

There was a gradual change from silt sediment in the inner fjord to predominantly rock at the outer Kongsfjorden (Table 1). There was a positive correlation ($r=0.61$, $P<0.05$) between rocky bottom and distance from the tidal glacier, in contrast with a negative correlation ($r=-0.61$, $P<0.05$) between soft bottom and distance from tidal glacier.

During this investigation the near-bottom salinity on the stations ranged from 32.90 to 34.35 psu while the temperature varied from 1.71°C to 4.99°C (Table 1). Salinity and temperature were slightly lower in the inner part of the fjord (Stations 4, 5 and 6).

The plot of PCA (Figure 4) (constructed using all the environmental data in Table 1) reflected the gradual change in environmental factors from the inner to the outer part of the fjord.

Occurrence of *Alcyonidium disciforme* correlated most strongly with the presence of clay and mud (Table 2).

Alcyonidium disciforme was present in 36 samples (22 stations) out of a total number of 300 samples (97 stations). The calculated frequency of occurrence was 12%. In total, 296 colonies were found: 32 from the grab, 58 from dredging, and 206 from SCUBA diving. The distribution of the species is illustrated in Figure 3, its presence was strictly restricted to the inner basin of Kongsfjorden. The outermost station where *A. disciforme* occurred was 14 (see Table 3), and it was recorded from 8 m to 240 m depth. The highest number of individuals was recorded from 10 m depth, the lowest at 9 m (Table 3). There was no significant correlation between the number of individuals and depth ($r=0.22$, $P<0.001$, $N=26$).

The wet mass of colonies ranged between 0.024 and 4.540 g (mean 0.51 g ±0.72 SD). The collected colonies were circular in outline and total colony diameter ranged from 0.85 to 47.00 mm (mean 14.26 mm ±13.11 SD). The correlation between colony diameter and wet mass was highly significant ($r=0.92$, $P<0.001$, $N=296$). This result is shown in Figure 5.

In general, colonies with a diameter >3 mm had started to develop the central hole. The central hole diameter of the specimens ranged from 0.14 to 19.00 mm (mean 4.87 mm ±4.69 SD). However, the largest colony without a central hole was 3.70 mm in diameter, while the smallest colony with it was 1.90 mm in diameter. Of the 296 colonies collected, 84.8% had developed a central hole whilst the remaining 15.2% had not.

Considering colonies without a central hole, the correlation between diameter and wet mass was significant ($r=0.87$, $P<0.001$, $N=45$). Considering colonies with a central hole, there was also a significant correlation between colony diameter and wet mass ($r=0.95$, $P<0.001$, $N=251$).

Six specimens were used in histological analysis, but only specimen NHM 2003.1.13.6 yielded useful sections. This was due to large amounts of sand particles being present inside the colonies causing sections to rip rather than be cut.

Measurements of autozooids and oocyte diameters are given in Table 4. A section of a piece of *A. disciforme* cut from the centre to edge of the colony and parallel to the oral surface is shown in Figure 6A. This reveals that the zooids were arranged in a particular pattern with autozooids at the outermost edge of the colony filled with sand particles, then reproductive zooids with oocytes further towards the colony centre. After reproduction the zooids appear to fill with degenerating material and were sloughed off from the colony centre, first creating and then enlarging the central hole. This corresponds to a certain extent with external observations on zooidal arrangement by Kvitek (1989), although he did not mention the existence of reproductive zooids in his account. Figure 6B shows the zooidal arrangements in slightly higher magnification. In Figure 6C it can be noted that there are cup-like extensions protruding from the edge of the colony surface. These extensions appear to be engulfing or enclosing sand particles and other inorganic material. In the figure these cup-like extensions can be seen in various stages of development. The autozooids behind the cup-like

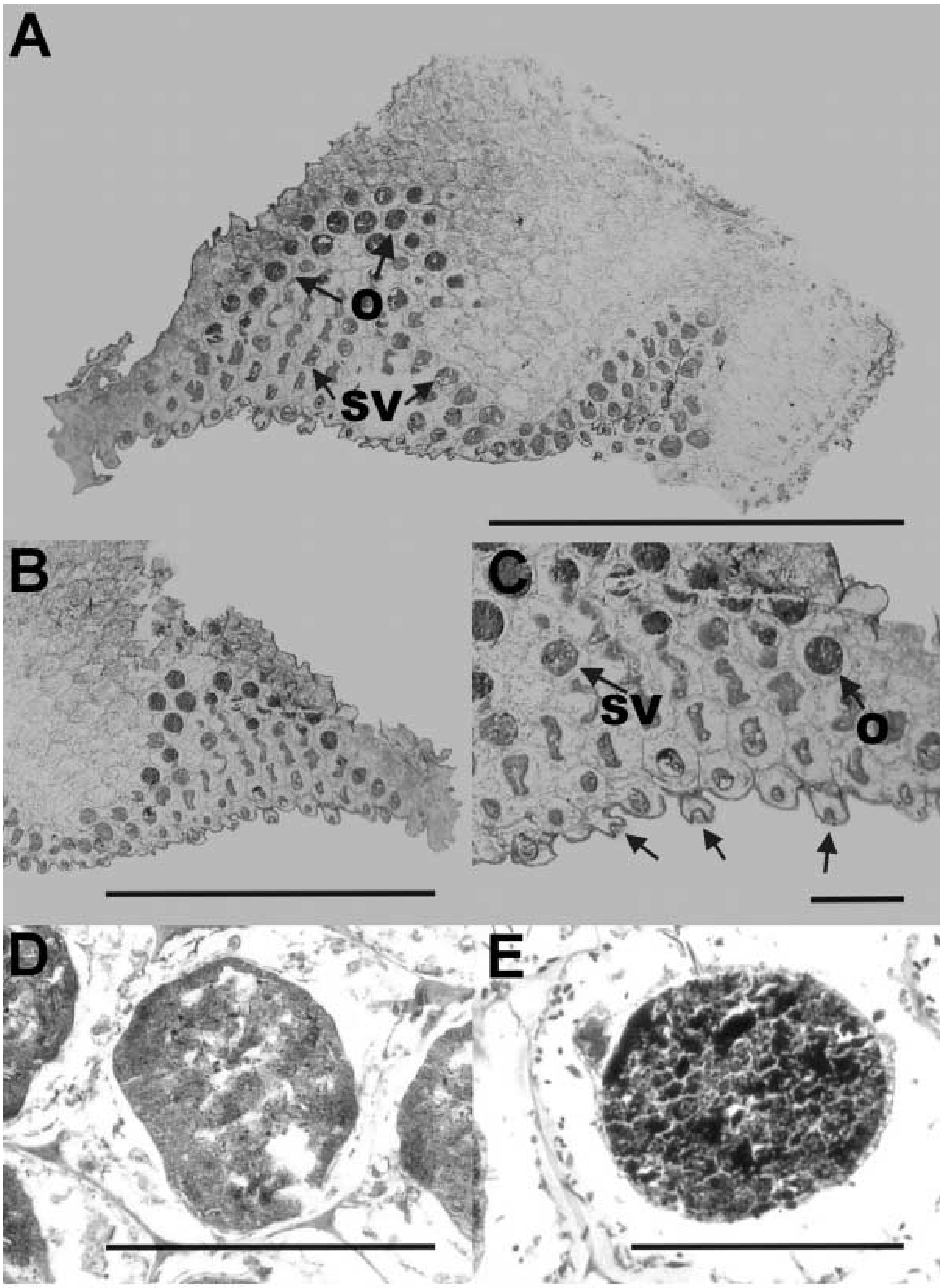

Figure 6. (A) Histological section through a piece of *Alcyonidium disciforme*, indicating arrangement of different zooid types: o, oocyte and sv, a sand vesicle; (B), histological section showing the arrangement of zooids at the edge of the colony with reproductive zooids in a band behind the autozooids; (C) section showing the zooids at the edge of the colony with cup-like extensions indicated by arrows, at different stages of sand particle collection, also arrowed is a single large oocyte (o) and a sand vesicle (sv); (D) section showing a sand vesicle in detail; (E) section showing a single large oocyte in detail. Scale bars: A, 0.75 cm; B, 0.5 cm; C–E, 0.3 mm.

extensions appear to contain vesicles consisting of sand particles bound by external cuticle. There were at least three layers of autozooids containing such sequestered sand vesicles, which were themselves quite large, approximately 0.3 mm in diameter. A typical sand filled vesicle is shown in Figure 6D. Further towards the inner part of the colony the autozooid bands changed to reproductive zooids and there was a clear band of zooids containing large lipid filled eggs, one per zooid and taking up almost the whole of the space inside the zooid (Figure 6B&E). Measurements of oocyte diameters are given in Table 4.

Table 4. *Measurements of zooids and oocytes in* Alcyonidium disciforme.

	Zooid length (mm) ±SD	Zooid width (mm) ±SD	Oocyte diameter 1 (mm) ±SD	Oocyte diameter 2 (mm) ±SD
Mean	0.44 ±0.06	0.34 ±0.05	0.37 ±0.04	0.33 ±0.05
Range	0.29–0.61	0.20–0.45	0.28–0.41	0.24–0.40
N	52	52	11	11

SD, standard deviation.

DISCUSSION

The main aim of this study was to provide a detailed description of the distribution and morphology of *Alcyonidium disciforme* found in Kongsfjorden, Svalbard, West Spitsbergen, in relation to local environmental parameters.

Results from the study show that there is no correlation between *A. disciforme* distribution and depth. The bryozoan occurred from shallow to very deep waters (8 to 240 m). Nordgaard (1912a,b, 1923) found this species at depths ranging from 5 to 408 m. Kluge's (1975) investigations also found no influence of depth on the distribution of the species. *Alcyonidium disciforme* in most cases lives in coastal areas (see Figure 1), with a few exceptional offshore occurrence (north of Norway—Nordgaard, 1900; Belgica Bank, East Greenland—B. Bader, personal communication). Thus the species' distribution encompasses a wide range of depths within the shelf area.

The local distribution of *A. disciforme* in the Kongsfjorden correlates with the presence of high concentrations of fine sediment and high sedimentation rates (see Tables 1 & 3, Figure 4). These conditions are mainly found in glacial bays situated in the inner parts of the fjord (Svendsen et al., 2002). The distribution of *A. disciforme* in other areas of Svalbard shows the same patterns as observed here at Kongsfjorden (Kirkpatrick, 1925; Włodarska et al., 1996; Węsławski unpublished data; personal observations). Of the 14 other localities with *A. disciforme* from Van Mijenfjorden and Isfjorden, all are characterized by a soft bottom and high sedimentation rate (IO PAS unpublished archival data); these are mainly glacial bays and river outlets. Station 8 (see Table 1) was characterized by strong sedimentation, which should favour occurrence of *A. disciforme*, but it was not present there. The bottom at Station 8 was covered with gravel. The combination of a high rate of sedimentation and a rocky bottom is the result of strong currents occurring in that part of the fjord (Svendsen et al., 2002) and was obviously unsuitable for *A. disciforme* colonies.

The glacial bays of Spitsbergen are characterized by a physically distinctive habitat; cold, dense near-bottom water, silt sediment, high mineral sedimentation rates, and a young seabed (Włodarska-Kowalczuk et al., 1998; Svendsen et al., 2002). The preference of *A. disciforme* for this distinctive habitat is shared by a range of other macrobenthos (Włodarska-Kowalczuk et al., 1998), dominated by deposit-feeding polychaetes and bivalves (Włodarska et al., 1996; Włodarska-Kowalczuk et al., 1998).

Alcyonidium disciforme occurs in a wide range of hydrological conditions. The shallow part of the Kongsfjorden is strongly influenced by freshwater input; here the salinity drops to 28 psu (Svendsen et al., 2002). This fluctuation does not seem to influence the abundance or presence of *A. disciforme*. The density of the species is quite high (1240 ind/m^2—see also Table 3) in the shallow area close to the glacier front at a salinity of 33.2 psu. On the other hand the species was also found at stations (see Table 3) which are under the influence of highly saline Atlantic waters (Svendsen et al., 2002).

Colony morphology in the Svalbard population was studied in detail. Gross measurements were made and positive correlations demonstrated between wet mass, colony diameter and central hole diameter. Development of the central hole of the colonies varies very much. Some of the colonies do not have a central hole at a diameter of 3.28 mm while others develop a hole at a diameter of 1.85 mm. Since most of the small colonies were collected from the same site (Station 4, Table 1), and were even part of the same samples, it is not easy to infer which environmental factors cause these variations. A significant correlation between the diameter of the whole colony and diameter of the central hole and between the weight and diameter of whole colony has also been noted in other Arctic regions: Barents Sea (Denisenko, 1990) and Chukchi-Bering Sea regions (Kvitek, 1989).

Our results show that there is a clear pattern of zooidal arrangement in *A. disciforme* which has not been previously described by histological methods. This study shows that one oocyte is brooded per zooid, and that the oocyte is relatively large (mean diameter 0.37 mm ±0.04 SD). This is an unusual strategy in *Alcyonidium* species as oocytes are generally brooded in clusters of four or more, for example, in *A. hirsutum*, *A. gelatinosum* and *A. polyoum* (Ryland & Porter, 2003).

Another notable feature of *A. disciforme* is its capacity to sequester sand particles and inorganic debris from its immediate environment by means of cup-like extensions of the outer body wall, which protrude from the outermost colony edge. These cup-like extensions are here observed surrounding masses of sand particles and subsequently the particles appear to be bound by external cuticle. This phenomenon of sand grain sequestering has also been reported in *A. diaphanum*, an erect subtidal *Alcyonidium* (Porter et al., 2001). It is not currently known as to why *A. disciforme* sequesters sand in this manner though one possibility is that the colony could be using the sand as ballast to help reorientate itself in the upright position following movement in the currents from one area to another.

There are many aspects of the basic biology and ecology of *A. disciforme* which remain to be fully elucidated. For example we are still far from establishing the life history (reproduction, astogeny) of this highly unusual species of *Alcyonidium*. Future studies are likely to reveal novel insights into new aspects of the life history of this unusual life form.

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