

M. A. Kendall · S. Widdicombe · J. M. Weslawski

A multi-scale study of the biodiversity of the benthic infauna of the high-latitude Kongsfjord, Svalbard

Received: 8 November 2002 / Accepted: 6 March 2003 / Published online: 16 April 2003
© Springer-Verlag 2003

Abstract A multi-scale study of patterns of biodiversity of the fauna of the upper basin of the Kongsfjord, Svalbard (78°55'N, 11°56'E) revealed that there were low rates of species turnover at distances in excess of 2 km. Where patterns within the assemblage were detected, they were largely the result of changing patterns of dominance within a restricted species pool of, for the most part, small-bodied animals. There are relatively few hierarchical studies of species turnover at the scale we have reported and all report different spatial relationships between faunal similarity and separation of the samples. It is strongly recommended that comparative measures of species turnover, estimates of the size of species pools, or comparative estimates of species diversity should include information on the spatial distribution, relative to habitat patchiness, of the samples considered.

Introduction

A major shortcoming of many marine benthic biodiversity studies has been their heavy reliance on a small number of point measures of diversity, and extrapolation from these to the whole assemblage (Gray 2000). This is despite the long acceptance of species-area curves (Sanders 1968) as a way in which the diversity of whole assemblages can be compared and as a way of assessing the number of samples needed for a meaningful estimate of species richness. Much effort has been directed at refining species-area relationships and the use of repeated sampling to gain estimates of the total number of

species within a sampling area (e.g. Chao 1987; Grassle and Maciolek 1992). In contrast, rather less effort has been devoted to considering the vital importance of the spatial distribution of the samples on which local estimates of diversity are based. Recent studies (Kendall and Widdicombe 1999; Somerfield and Gage 2000) suggest that the optimal way in which a small number of samples can be distributed in order to maximise estimates of local species richness will vary from place to place. These studies further suggest that existing estimates of local diversity that lack information on inter-sample distance must be treated with caution.

To address criticisms concerning the inadequacy of scale and establish local patterns of species turnover, larger, spatially referenced, data sets need to be examined using more appropriate measures of diversity. In this paper, a new, large (52 samples) data set, collected from an Arctic glacial basin using a strongly structured, multi-scale-sampling scheme, is analysed to examine species-area and similarity-distance relationships among the benthic infauna. To minimise turnover in species composition resulting from changes in habitat, it was intended to describe patterns of variability within an area that was as physically homogeneous as possible.

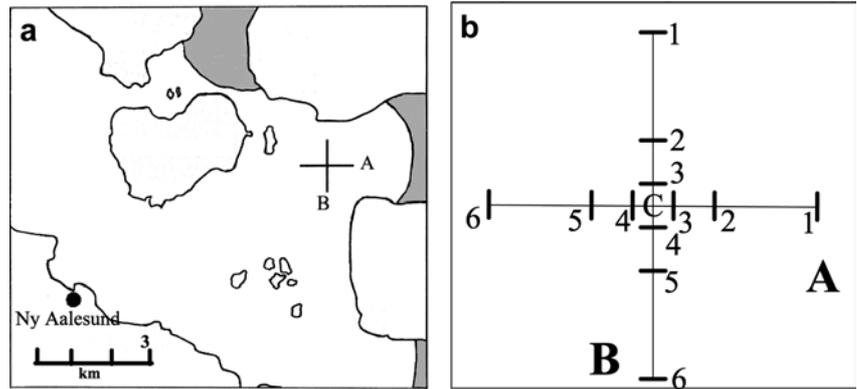
Materials and methods

The data set comes from the inner basin of the Kongsfjord, Spitsbergen, a high-latitude (78°55'N, 11°56'E) environment influenced by boreal water masses (Hop et al. 2002). Previous sampling (J.M. Weslawski, unpublished work) had suggested that this basin was faunistically homogeneous, perhaps as a result of the heavy glacial sedimentation that affects its whole area (Fig. 1). The innermost sampling site (Fig. 1) was situated 2,100 m from the retreating Conwaybreen branch of the Kongsbreen Glacier, which annually deposits 5–10 cm of new sediment to the sea bed at a distance of 10 km from the glacial front (Elverhøi et al. 1983). The study area was chosen to provide the most uniform possible combination of depth and sediment granulometry. Depth varied between 50 and 70 m while the sediment at all stations was soft red mud (containing >80% by weight of particles finer than 63 µm; M. Zajaczkowski, personal communication). Sampling did not

M. A. Kendall (✉) · S. Widdicombe
Plymouth Marine Laboratory, Prospect Place, Plymouth,
PL1 3DH, UK
E-mail: mak@pml.ac.uk

J. M. Weslawski
Institute of Oceanology, Polish Academy of Sciences, 55,
Powstancow Warszawy Street, Sopot, 81-712, Poland

Fig. 1a, b Map of the inner basin of the Kongsfjord (78°55'N, 11°56'E) indicating transects A and B. Stations are at distances of 50 m, 450 m and 1,220 m from the central point



attempt to describe patterns of diversity in the whole fjord, which has a number of clearly separate faunistic zones (M. Włodarska-Kowalczyk in Hop et al. 2002).

Sampling was carried out in July 1997, from R.V. Oceania of the Polish Academy of Sciences, along two orthogonally intersecting transects (Fig. 1) each with six stations and a common midpoint. Transect A was set perpendicular to the glacial front while transect B was a constant distance from it. The separation of stations (50, 450 and 1,220 m) from the central point was intended to provide as wide a range as possible of spatial comparisons of species turnover. At each station, four replicate samples were taken using a 0.1-m² van Veen grab. Station positions were fixed using GPS navigation and it is assumed that all samples at a given station were within a circle of radius 50 m.

Samples were washed over a 0.5-mm square-mesh sieve and fixed in formalin onboard ship. Onshore, the fixed samples were washed and preserved in 70% alcohol. The fauna was picked from the sediment debris under a stereo-microscope and all animals were identified to the lowest practical taxon. There were a number of instances where either damage or the presence of juvenile animals prevented consistent identification and enumeration at the species level. In these cases, it was necessary to combine records at the lowest consistent taxonomic level for multivariate analysis.

Multivariate analyses and sample-diversity calculations were performed using the PRIMER package (Clarke 1993). A primary aim of the study was to relate faunal similarity to the distance separating any pair of samples. To achieve this, the Bray-Curtis similarity matrix was decomposed and values of similarity were grouped according to the distance separating the samples from which they were derived. In this way, plots of similarity against distance of separation could be achieved. Data were analysed without transformation by the use of $\sqrt{\cdot}$, $\sqrt[3]{\cdot}$ or presence/absence transformations. While the outputs of untransformed analyses are

dominated by the commonest species, in presence/absence transformed analyses all species have the same influence. One-way ANOSIM (Clarke and Green 1988) was used to test for significant differences between the fauna at the various distances of separation.

Although previous studies suggested faunal homogeneity, the possibility that patterns within the data might be related to glacial discharge was not discounted. It was allowed for in the sampling design and examined using a seriation test based on the RELATE procedure (Clarke and Warwick 1994). This test takes the faunal dissimilarity matrix and compares it with a second matrix constructed on the assumption that, along an environmental gradient, dissimilarity will change serially from station to station. Replicate samples are assumed to be totally similar (score 0); dissimilarity then increases with distance until a score of 4 is allocated to sites with the maximum separation. The two matrices are compared using Spearman rank correlation (K.R. Clarke, unpublished work).

Results

The fauna

Individual samples contained between 300 and 600 individuals, and were dominated by small-bodied polychaete worms, protobranch bivalves and tanaid crustaceans. Table 1 lists all species represented by more than 30 individuals. Among the polychaetes, the small sabellid *Chone paucibranchiata* was the most common taxon, followed by paraonids (*Levinsenia gracilis* and

Table 1 Abundance-ranked list of species represented by more than 30 individuals in all samples collected

Annelida	Rank	Mollusca	Rank	Arthropoda	Rank	Other taxa	Rank
<i>Chone paucibranchiata</i>	1	<i>Yoldiella lenticulata</i>	2	<i>Sphyrapus anomalus</i>	3	<i>Nemertea indet</i>	26
Cirratulidae	4	<i>Thyasira</i> spp	9	<i>Eudorella emarginata</i>	7	<i>Alcyonidium disciformae</i>	29
<i>Levinsenia gracilis</i>	5	<i>Yoldiella fraterna</i>	11	<i>Typhlotanais finmarchicus</i>	10		
<i>Aricidea</i> sp1	6	<i>Nuculana tenuis</i>	13	<i>Leptognathia breviremis</i>	14		
<i>Cossura longocirrata</i>	8	<i>Axinopsida orbiculata</i>	15	<i>Pseudotanais forcipatus</i>	20		
<i>Lumbrineris mixochaeta</i>	12	<i>Cuspidaria cuspidata</i>	18				
<i>Polycirrus arcticus</i>	16	<i>Similipecten groenlandicus</i>	21				
<i>Agalophamus malmgreni</i>	17	<i>Nuculana pernula</i>	25				
<i>Terebellides stroemi</i>	19						
<i>Heteromastus filiformis</i>	22						
<i>Langerhansia cornuta</i>	23						
<i>Prionospio steenstrupi</i>	24						
<i>Galathowenia oculata</i>	27						
<i>Nephtys ciliata</i>	28						

Aricidea spp.) and a complex of cirratulid species dominated by *Chaetozone setosa*. In the majority of samples, the biomass dominant was the nephthiid *Agalophamus malmgreni*; otherwise, errant species were only represented regularly by small individuals of *Lumbrineris mixochaeta*. *Yoldiella lenticulata* and *Y. fraterna* were the most common bivalves. In comparison with other studies of Svalbard fjords (Kendall and Aschan 1993; Wlodarska et al. 1996) the tanaid crustaceans *Sphyrapus anomalus*, *Leptognathia longiremis* and *Peraeospinus mixtus* were all particularly abundant.

A total of 74 taxa were recorded in 52 samples. A species accumulation curve is presented as Fig. 2 that continues to rise, suggesting that the species pool is not fully sampled. With the exception of station A1, the mean number of species per sample in transect A was relatively consistent at 29.5 ± 1.2 (95% CI). At station A1, the mean abundance fell to 18.5 ± 5.4 . On the central part of transect B, parallel to the glacial front, the number of species (29.6 ± 3.1) was not significantly different from the greater part of transect A. However, at its extremes (B1 and B6), numbers were lower (22.5 ± 4.1 and 22 ± 1.2 species, respectively). Mean Shannon diversity (\log_e) in stations within 500 m of the transect intersection (stations A2–A5 and B2–B5) was 2.43 ± 0.03 . Of the outermost stations, A6, B1 and B6 did not differ significantly from the central area but station A1 was substantially less diverse (1.52 ± 0.3).

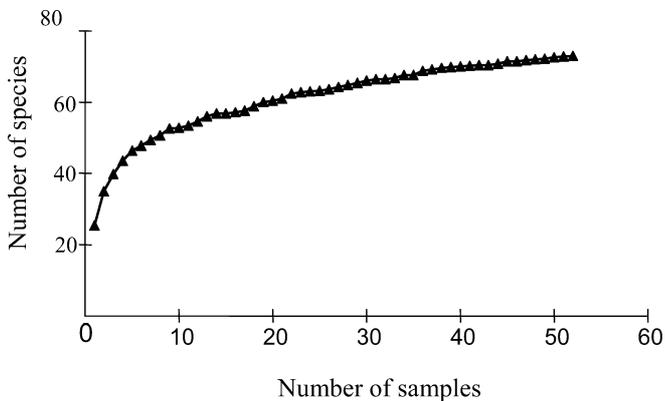


Fig. 2 Species accumulation curve, smoothed on the basis of 20 random picks

Spatial patterns in the fauna

One-way ANOSIM was employed to test for patterns in the fauna; the two transects were examined separately. The significance of the results of the analysis was highly dependent on the degree to which data were transformed. For transect A, ANOSIM for untransformed data showed 12 of 21 pair-wise comparisons differed significantly ($P < 0.05$). The number of significant differences fell as the strength of the transformation increased until presence/absence transformed data indicated only a single significant difference between stations. For transect B, there was a similar change in the number of significant results as the strength of data transformation was increased. The changes in patterns of similarity with increasing strength of transformation indicate that, although the relative distribution of a small number of dominant species might vary, the species pool is relatively consistent.

Figure 3 examines the relationship between the Bray-Curtis similarity of any pair of samples and the distance separating them. It uses all possible pairs to produce similarity-distance plots for data that are untransformed (Fig. 3a) and $\sqrt{\sqrt{\quad}}$ transformed (Fig. 3b). For untransformed data, mean similarity within samples taken at a single station (replicates assumed to be separated by 50 m) was a little over 70%, a level that was, on average, maintained over distances of up to 500 m. With greater separation, inter-sample similarity declined but not below 50%. Slightly higher similarities were recorded for transformed data, emphasising the low levels of species turnover between samples.

In view of the greater dissimilarity at sites A1 and B1 and the possibility that this might be a result of proximity to the glacier, spatial trends in community structure along each transect were examined using multivariate tests of seriation. Results are summarised in Table 2. Each analysis showed significant seriation. The significance of the correlation coefficient, R , declines substantially for presence/absence transformation. There was a progressive change in the composition of the fauna away from site A1 on transect A. The same was true away from site B1 on transect B. As it was possible that outermost stations might have had a disproportionate effect on the outcome of the analyses, they were re-run with the outermost stations (A1, A6, B1, B6) omitted. Table 2 shows

Fig. 3a, b The relationship between mean Bray-Curtis Similarity ($\pm 95\%$ CI) and the spatial separation of any pair of samples for a untransformed and b $\sqrt{\sqrt{\quad}}$ transformed data

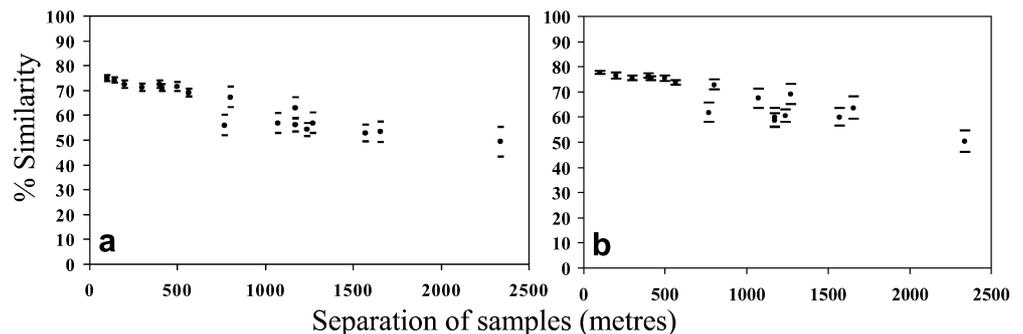


Table 2 Results of seriation analysis for the full data set and sites 1–9 only

Sites 1–9 only	Transect A		Transect B	
	R	Significance (%)	R	Significance (%)
Full data set				
Untransformed	0.53	0.0	0.59	0.0
√ transformed	0.55	0.0	0.61	0.0
√√ transformed	0.47	0.0	0.49	0.0
Presence/absence transformed	0.33	1.0	0.29	1.9
Untransformed	0.41	0.0	−0.03	57.6
√ transformed	0.48	0.0	0.03	37.0
√√ transformed	0.35	0.1	0.01	43.6
Presence/absence transformed	0.15	5.8	−0.02	55.3

a substantial change in values of significance; although seriation can still be detected perpendicular to the glacial front (transect A), no significant pattern could be detected parallel to it (transect B). Despite the high homogeneity of the fauna (Fig. 3), there are still subtle trends within the data matrix. The serial change in fauna away from the glacial front on transect A is principally the result of changes in patterns of dominance rather than being due to species substitutions or losses. Only the stations closest to the glacier are notably less species-rich.

The nature of faunal change along transect A can be seen if plots of the abundance of some of the dominant taxa are examined (Fig. 4). Cirratulid polychaetes were at their most abundant at the station closest to the glacier (station A1) with numbers almost 50% higher than elsewhere along the transect. Other species (*Cossura* sp. and *Levinsenis gracilis*) showed low abundance close to the glacier but then increased at a single station before declining. A further group, comprising the three tanaids, *Leptognathia longiremis*, *P. mixtus* and *S. anomalus*, as well as the cumacean, *Eudorella emarginata* and the polychaete *Aricidea*, were uncommon at the innermost stations but maintained moderate densities thereafter. Finally, *Lumbrineris*, *Yoldiella* spp. and *Thyasira* sp. all maintained a pattern of steady increase along the transect. Of the dominant species, only the small sabellid polychaete *Chone paucibranchiata* showed no clear response to the disturbance gradient away from the glacier.

Discussion

In this paper, we demonstrate high faunal homogeneity in the upper Kongsfjord basin; two benthic sediment samples taken 500 m apart are, on average, as similar to each other as samples taken at the same station. Even at the maximum extent of our study (in excess of 2 km), samples were more than 50% similar. These values of similarity are based on untransformed data and so are principally influenced by patterns of abundance within the dominant species. A consideration of √√ trans-

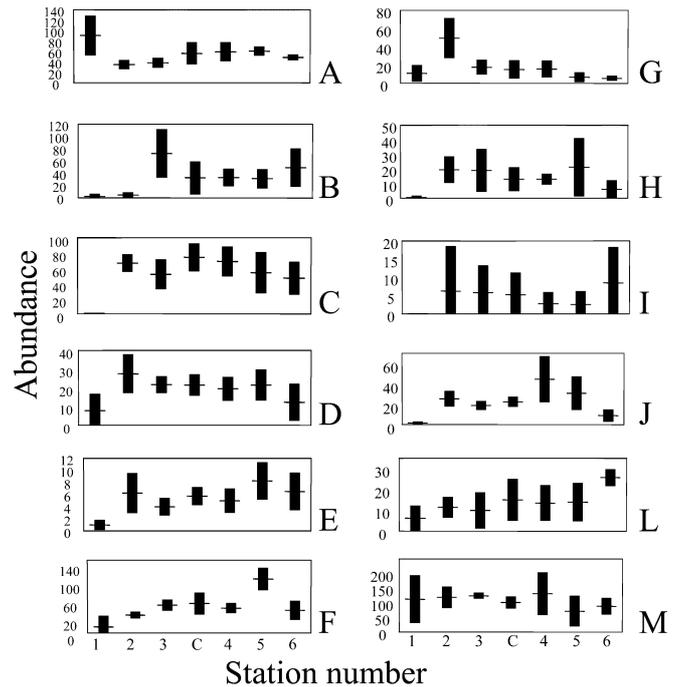


Fig. 4 Patterns of abundance of dominant species along transect A. The bar depicts mean abundance $\pm 95\%$ CI (A all cirratulids; B *Levinsenis gracilis*; C *Sphyrapus anomalus*; D *Eudorella emarginata*; E *Lumbrineris mixochaeta*; F All *Yoldiella*; G *Cossura* sp.; H *Peraeospinus mixtu*; I *Leptognathia longiremis*; J *Aricidea* spp.; L *Thyasira gouldi/dunbari*; M *Chone paucibranchiata*)

formed data causes the fauna to appear even more homogeneous. Faunal homogeneity on the scale of the transects described in this paper extends to the remainder of the inner fjord basin (Hop et al. 2002).

Within the high overall homogeneity of the inner basin of Kongsfjord, it appears that effects on diversity of local-scale disturbances are lost in the general noise created by high, basin-scale, sedimentation. Local diversity patterns can only be demonstrated in the areas immediately adjacent to individual glaciers. Nevertheless, even in such a faunally homogeneous area, a small number of replicate samples taken within a single station would not give a good approximation of the species richness of the study site. Four samples taken randomly in the study area would give about 45% of the species present (Fig. 2) but if samples were grouped at a single location, high within-station similarity (Fig. 3) would substantially reduce the number of species caught. A small number of samples taken in any one location would substantially underestimate the size of the species pool.

If in the homogeneous sediments of the upper basin of Kongsfjord, species richness cannot be estimated by a relatively small number of samples, doubts must be raised concerning existing previous estimates of polar benthic diversity. Our data support Gray's (2000) assertion that, in many comparative studies of diversity, the area sampled is often too small and the diversity measures employed inappropriate. If the conclusions of

previous comparative studies are weakened, then it is important to stress that, in the majority of cases, small samples grouped closely together would significantly underestimate the species composition of a broader area. An earlier study of benthic diversity in Svalbard (Kendall and Aschan 1993) made comparisons with benthic diversity at lower latitudes and showed little latitudinal difference in sample diversity. Bearing in mind the results presented above and those of similar studies (Kendall and Widdicombe 1999; Somerfield and Gage 2000), it is likely that while diversity in Svalbard was underestimated, so too was that at lower latitudes. We conclude that truly broad-scale comparisons of species richness need larger numbers of samples collected within well-defined areas using explicitly described sampling protocols. A similar conclusion has recently been reached by Gray (2002). Future attempts at identifying broad-scale patterns in benthic biodiversity must be based on spatially structured sampling informed by an appreciation of the patchiness of the benthic seascape. There are few studies in existence that meet such criteria.

Although the benthic species of the inner basin of the Kongsfjord prosper in an area highly disturbed by high sedimentation, none that are abundant have life-history traits that might be considered typically opportunistic. Close to the glacier, cirratulid polychaetes, principally *Chaetozone setosa*, were numerically dominant. This species is a burrowing selective-surface deposit feeder (Dahle et al. 1998) and is broadly distributed in muddy sediments in shallow waters of boreal seas (e.g. Buchanan 1993; Olsford and Hasle 1993; Craeymeersch et al. 1997) and in offshore Arctic seas (Kendall 1996; Dahle et al. 1998) and is characteristic of many other Arctic fjords (Kendall and Aschan 1993; Holte and Gulliksen 1998; Wlodarska-Kowalczyk et al. 1998). In Greenland, Curtis (1977) reported that the species had lecithotrophic development and probably spawned during the winter months. A number of small-bodied polychaetes, particularly *Cossura* sp., *Levinsenia gracilis* and *Chone paucibranchiata*, were also tolerant of sedimentation. The first two taxa have frequently been recorded in other fjords (Holte and Gulliksen 1998) and shallow disturbed environments. *Cossura* species have direct development and may well be capable of continuous reproduction (Blake 1993). In laboratory studies of disturbance, *Cossura* maintained its numbers well in a high-disturbance regime (Widdicombe and Austen 1999). The biology of *Levinsenia* is little known, while in common with other small-bodied sabellids (Wilson 1991), species of the genus *Chone* are probably polytelic and produce brooded lecithotrophic eggs. In the inner Kongsfjord, three species of tanaid crustaceans, as well as the cumacean *E. emarginata*, all prosper under high turbidity and heavy sedimentation. All of these animals produce low numbers of offspring that are brooded. Finally, in common with other glacial bays (Wlodarska et al. 1996), the inner basin of the Kongsfjord has a

substantial population of small protobranch bivalves of a number of species of the genus *Yoldiella*.

It is significant that among the species that are successful in the upper Kongsfjord, are a number that have been recorded as responding to disturbance elsewhere. The most successful, *Chaetozone setosa*, does not have the biological characteristics to exploit short-term creation of space; it is a species that most probably has a single breeding period and limited planktonic dispersion (Curtis 1977); it appears it is fitted to resist disturbance rather than responding to it by reproduction. Similarly, other species that are among the dominants within the fjord have low fecundity and limited ability to disperse. The decline in *Chaetozone* away from the glacier suggests that a trade-off exists between tolerance and competitive ability, in just the same way as along a pollution or disturbance gradient at lower latitudes. In considering disturbed environments, it is easy to concentrate on the role of recruitment of true opportunists from the plankton and overlook species that have either been displaced or have resisted the perturbation. Although Pearson and Rosenberg (1978) made this distinction, it has subsequently been largely overlooked.

Acknowledgements The work contained in this paper was funded in part by grants from the European Union's Foundations Large Scale Facility (Ny Aalesund) and from UK DEFRA (project no. AE1113). It was partly funded by the UK Natural Environment Research Council through the Plymouth Marine Laboratory research programme Scaling Biodiversity and the Consequences of Change (SBC). We would like to thank the Polish Institute of Oceanology for providing time aboard RV Oceania, and Slawek Kwasniewski, Piotr Kuklinski and Zosia Legezynska for help in collecting the samples. Bob Clarke advised on the sampling design/data analysis and provided invaluable comments on the manuscript. Maria Wlodarska Kowalczyk also provided valuable comments on various drafts of the manuscript. Magda Blazewicz supplied identities for the tanaids. Thanks also go to Haaken Hop of the Norwegian Polar Institute and Nick Cox of British Antarctic Survey for help in arranging the visit to Svalbard and hospitality while there.

References

- Blake JA (1993) Life history analysis of five dominant infaunal polychaete species from the continental slope off north Carolina. *J Mar Biol Assoc UK* 73:123–141
- Buchanan JB (1993) Evidence of benthic pelagic coupling at a station off the Northumberland coast. *J Exp Mar Biol Ecol* 172:1–10
- Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43:783–791
- Clarke KR (1993) Non parametric multivariate analyses of changes in community structure. *Aust J Ecol* 16:117–143
- Clarke KR, Green RH (1988) Statistical design and analysis for a biological effects study. *Mar Ecol Prog Ser* 46:213–226
- Clarke KR, Warwick RM (1994) Changes in marine communities; an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Craeymeersch JA, Heip CHR, Buijs J (1997) Atlas of North Sea benthic infauna. Based on the 1986 North Sea Benthos Survey. International Council for the Exploration of the Sea (ICES) Coop Res Rep 218:8

- Curtis MA (1977) Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia* 16:9–58
- Dahle S, Denisenko SG, Denisenki NV, Cochrane SJ (1998) Benthic fauna in the Pechora Sea. *Sarsia* 83:183–210
- Elverhøi A, Lonne O, Seland R (1983) Glaciomarine sedimentation in a modern fjord environment, Spitsbergen. *Polar Res* 1:127–149
- Grassle JF, Maciolek NJ (1992) Deep-sea species richness—regional and local diversity estimates from quantitative bottom samples. *Am Nat* 139:313–341
- Gray JS (2000) The measurement of marine species diversity with an application to the benthic fauna of the Norwegian continental shelf. *J Exp Mar Biol Ecol* 250:23–49
- Gray JS (2002) Species richness in marine soft sediments. *Mar Ecol Prog Ser* 244:285–297
- Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar-Biol* 19:375–382
- Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Włodarska-Kowalczyk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-A, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, Prisco di G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res* 21:167–208
- Kendall MA (1996) Are Arctic soft sediment macrobenthic communities impoverished? *Polar Biol* 16:393–399
- Kendall MA, Aschan M (1993) Latitudinal gradients in the structure of macrobenthic communities: a comparison of arctic tropical and temperate sites. *J Exp Mar Biol Ecol* 172:157–170
- Kendall MA, Widdicombe S (1999) Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediment. *J Exp Mar Biol Ecol* 237:127–140
- Olsgard F, Hasle JR (1993) Impact of waste from titanium mining in benthic fauna. *J Exp Mar Biol Ecol* 172:185–214
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. *Oceanogr Mar Biol Annu Rev* 16:229–311
- Sanders HL (1968) Marine benthic diversity; a comparative study. *Am Nat* 102:243–282
- Somerfield PJ, Gage JD (2000) Community structure of the benthos in Scottish Sea-lochs. IV. Multivariate spatial pattern. *Mar Biol* 136:1133–1145
- Widdicombe S, Austen MC (1999) Mesocosm investigation into the effects of bioturbation on the diversity and structure of a sub-tidal macrobenthic community. *Mar Ecol Prog Ser* 189:181–193
- Wilson WH (1991) Sexual reproductive modes in polychaetes; classification and diversity. *Bull Mar Sci* 48:500–516
- Włodarska M, Weslawski JM, Gromisz SA (1996) Comparison of the macrofaunal community structure and diversity in two arctic glacial bays—a 'cold' one off Franz Josef Land and a 'warm' one off Spitsbergen. *Oceanology* 38:251–283
- Włodarska-Kowalczyk M, Weslawski JM, Kotwicki L (1998) Spitsbergen glacial bays macrobenthos; a comparative study. *Polar Biol* 20:66–73