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Animal community structure as a function of stream size

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Abstract

The species-area relationship of the island biogeography theory was calculated for macroinvertebrates in 22 coastal, adjacent streams. A z-value of 0.19 was obtained. The low z-value was probably a consequence of the short distances between streams as well as high dispersal rates. In addition, a cluster analysis based on the dissimilarity of species assemblages showed that stream size was of prime importance in categorizing the streams. To a smaller extent water quality affected the community structure in the streams.

Introduction

A variety of abiotic factors have been shown to affect the occurrence of stream-living invertebrates (see Hynes 1970 for references). Abiotic factors alone, however, seldom explain the occurrence of certain species in closely situated streams of similar size.

The diversity of food available to macroinvertebrates varies along water courses, and consequently different trophic guilds dominate at different sections (Malmqvist *et al.*, 1978; Vannote *et al.*, 1980; Hawkins & Sedell, 1981). The increased variety of food and microhabitats will often support more species in downstream sections compared to small headwater streams (Mackay, 1969; Friberg *et al.*, 1977). However, shifts in food availability over short distances in small streams are less likely to be pronounced.

Another factor that affects community structure is area of habitat available to biota (MacArthur & Wilson, 1967). Coastal river systems may be regarded as habitat islands from the biogeographical point of view as shown for freshwater mussels in North American rivers (Sepkoski & Rex, 1974). The interaction between area and distance from source rivers was found to be crucial in determining the number of species.

The aim of the present study was to analyse the differences in faunal composition between small, closely situated coastal streams exposed to similar abiotic conditions, and between which dispersal should be high since most of the invertebrate species have winged stages. In the analyses emphasis was put on the effects of stream size in structuring the benthic animal communities.

Study area

The investigation was carried out in 22 Bornholm streams in June 1982. Bornholm is a Danish island situated in the Baltic between Sweden and Poland. The area of the island is 587 km^2 and the closest mainland (southern Sweden) is situated some 26 km away.

All the streams investigated fall into the sea along the northeastern coast of the island (Fig. 1). The distance between the two outermost streams is about 30 km, and the maximum distance between two adjacent streams does not exceed 1.5 km. Sampling was always performed near the mouths of the streams.

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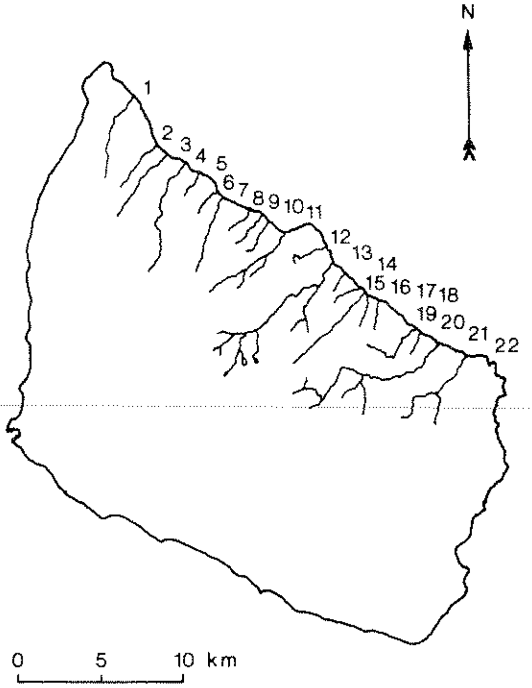

Fig. 1. The position of the study streams in Bornholm.

The moraine covered bedrock in this part of the island mainly consists of gneiss and granite. The streams run through farmland, some also through deep ravines shaded by elm (*Ulmus glabra*), ash (*Fraxinus excelsior*), and beech (*Fagus silvatica*). The bottom substrate at the study sites was comparatively uniform, consisting of stones, gravel, and sand, the only exceptions being the sites in streams Nos. 1 and 22, where the bottom was mainly rocky outcrop. Environmental features of the study sites are summarized in Table 1.

Material and methods

The average width, depth, and presence of aquatic macrophytes were measured at each site. Nitrate and conductivity were measured as an estimate of diffuse farmland pollution affecting the streams. The macroinvertebrate fauna was sampled by kick sampling with hand nets (0.6 mm mesh size), and also by direct picking from stones. Sampling time was about 2 man-hours per study site. The animals were immediately preserved in ethanol.

Table 1. Environmental features at the study sites of the streams investigated. A + sign denotes heavy, (+) moderate, and - no shading.

Stream no.		Total area (10^3 m^2)	Width (m)	Depth (cm)	Shading (+, -)	Fontinalis sp. (F) Cladophora sp. (C)	pH	κ_{20} (mS m^{-1})	NO$_3$ (mg l^{-1})
1	Kampelökke Å	4.4	1.5	12	-	(C)	8.3	55	4.1
2		1.2	0.7	8	-	(C)	8.3	68	6.7
3	Möllebaek	1.8	0.8	4	(+)	(C)	8.3	58	7.0
4	Tejn Å	4.7	1.2	8	+		8.4	61	9.0
5		0.5	0.6	5	+		8.4	63	9.0
6		1.7	1.9	13	+		8.4	50	6.7
7	Sperlinge Å	4.6	1.9	9	(+)		8.4	54	3.4
8		0.7	0.7	6	+		8.0	80	9.8
9	Vasebaek	1.6	1.0	4	(+)	(C)	8.4	57	7.3
10		0.4	0.5	2	(+)	(C)	8.0	63	5.2
11	Bobbeå	4.8	1.2	5	(+)	(F) (C)	8.2	46	2.8
12	Melsted Å	2.1	1.6	5	+		8.3	59	4.8
13	Kobbeå	10.4	2.6	13	+		8.4	55	3.9
14		0.5	0.7	3	+		8.2	67	7.6
15		0.1	0.1	3	+	(F)	8.3	57	5.2
16	Kelse Å	6.4	2.0	8	+	(C)	8.3	56	3.2
17		0.6	0.5	5	+		8.3	60	8.3
18		0.4	0.6	3	+		8.2	55	4.6
19		5.0	2.3	5	+		8.1	54	5.4
20		1.2	1.1	9	+	(F)	8.2	53	6.4
21	Gyldenså	12.8	2.1	9	+	(F) (C)	8.0	49	2.8
22		7.6	2.1	4	+	(F) (C)	7.9	51	1.5

Stream area was approximated to a triangle, the base of which was stream width near the mouth. The height of the triangle was the length of the stream, exclusive of tributaries, as measured from a map of Bornholm (1:60 000, Geodaetisk Institut, Copenhagen 1969).

In order to identify patterns in the community structure of the 22 streams, they were classified into discrete categories. This analysis involved three different methods, all computed by use of the CLUSTAN program (Wishart, 1978). Each method used a different similarity coefficient: squared Euclidian distance (dissimilarity), similarity ratio (Jaccard, similarity), and nonmetric (Bray-Curtis, dissimilarity). Results based on a matrix derived from squared Euclidian distances followed by hierarchical clustering using Ward's method yielded the best resolution, although patterns produced by the other two methods were similar. The squared Euclidian distance equals the sum of unique species to site 1 and site 2, divided by the total number of species of the two sites combined.

To estimate the status of the macroinvertebrate communities with respect to pollution, saprobic values were calculated for each site according to Mauch (1976).

The theory of island biogeography (MacArthur & Wilson 1967) established the relationship between the number of species of true or habitat islands (S) and island area (A) as

$$S = C \cdot A^{z},$$

where C and z are constants. The value of z usually ranges between 0.20–0.35. A high z-value is characteristic of groups of islands in which the number of species increases rapidly with increasing island area.

Results

Fifty-seven taxa were collected. Number of taxa at individual streams ranged between 8 and 24 (Table 2). Trichoptera had the highest number of species followed by Coleoptera.

A significant ($p < 0.001$) positive relationship was established between the number of taxa at each study site and the stream area (Fig. 2). The z and C values were estimated as 0.19 and 3.60, respectively.

Figure 3 demonstrates the results of the cluster analysis. Two clusters formed. In cluster 1 (stream Nos. 4, 6, 7, 11, 13, 16 & 21) a number of species

Table 2. Aquatic macroinvertebrates obtained in the streams investigated.

	Stream no.																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Turbellaria																						
Dendrocoelum lacteum				x		x					x						x		x			x
Gastropoda																						
Lymnea palustris					x										x							
Lymnea peregra										x			x		x							
Ancylus fluviatilis	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x		x	x	x	x
Lamellibranchiata																						
Pisidium sp.										x											x	
Oligochaeta																						
Tubificidae indet.			x			x	x	x			x	x	x					x	x		x	
Chaetogaster limnaei				x			x				x	x	x									
Eiseniella tetraedra				x			x					x		x	x		x					
Hirudinea																						
Glossiphonia complanata	x	x					x		x	x	x	x	x						x	x		x
Helobdella stagnalis												x										x
Erpobdella octoculata										x	x	x	x					x	x		x	x
Dina lineata																		x			x	x
Hydracarina in det.																						x
Isopoda																						
Asellus aquaticus								x										x				x

Table 2. (Continued).

	Stream no.																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Amphipoda																						
Gammarus pulex	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	
Ephemeroptera																						
Siphlonurus sp.																x						x
Baëtis rhodani	x	x	x	x	x	x	x		x	x	x	x	x		x	x	x		x	x	x	
Baëtis vernus	x				x		x	x	x	x	x	x	x		x	x			x	x	x	x
Ephemera danica						x	x				x											
Plecoptera																						
Nemoura cinerea															x							
Leuctra fusca			x	x		x			x				x									
Leuctra hippopus											x											
Heteroptera																						
Gerris gibbifer													x									
Velia caprai			x									x					x		x	x		
Coleoptera																						
Haliplus lineatocollis																						x
Copelatus haemorrhoidalis																		x				
Agabus sp.														x								
Ilybius sp.														x	x							x
Haenydra gracilis		x		x																		
Helophorus sp.													x		x							
Anacaena globulus						x						x		x	x							
Elmis aenea	x	x	x	x	x	x					x	x				x						
Limnius volckmari			x			x							x									
Helodes minuta					x							x								x		
Trichoptera																						
Rhyacophila fasciata	x	x	x	x	x	x	x		x	x	x					x	x		x	x	x	x
Rhyacophila nubila											x		x									
Agapetus fuscipes				x		x	x														x	
Hydropsyche siltalai				x		x	x				x	x	x			x					x	
Plectrocnemia conspersa	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Polycentropus flavomaculatus							x				x		x			x					x	
Limnephilus lunatus																		x				
Limnephilus sp.		x																			x	
Potamophylax cingulatus				x		x	x				x	x	x				x		x		x	
Potamophylax latipennis				x		x	x		x							x						
Halesus radiatus				x		x	x						x			x					x	
Stenophylax permistus																x						
Chaetopteryx villosa		x		x	x	x	x	x	x		x		x			x	x			x	x	
Silo pallipes				x		x	x				x		x			x					x	
Sericostoma personatum		x		x		x	x		x		x		x				x			x	x	
Diptera																						
Tipula sp.					x													x				
Dicranota sp.		x	x			x							x	x		x	x		x			
Eloeophila sp.						x																
Pilaria sp.					x																	
Scleroprocta sp.				x												x						
Simuliidae indet.	x		x		x	x	x				x	x		x					x			x
Chironomidae indet.	x	x	x	x		x	x	x		x	x	x	x	x		x	x	x	x	x	x	x
Forcipomyia sp.					x					x												
Σ taxa:	10	13	13	21	14	24	21	8	11	12	23	19	24	9	10	18	13	10	15	12	20	16

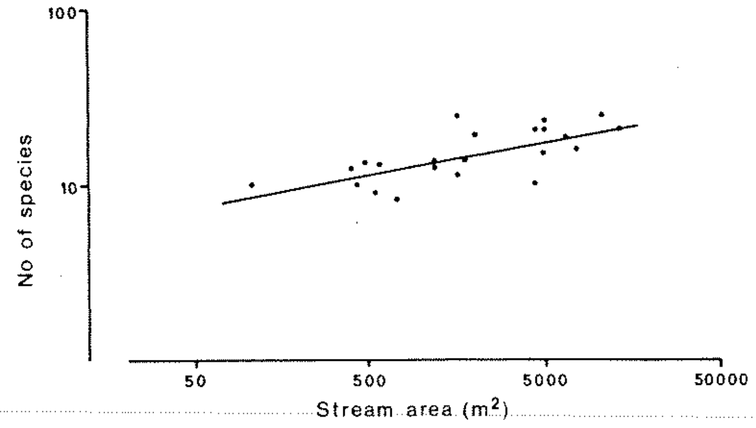

Fig. 2. The relationship between number of taxa and stream area y = 0.185x + 1.28 (r = 0.685, P < 0.001).

occurs that are not represented in cluster 2. These species include *Silo pallipes* that was found in all streams belonging to cluster 1. Also *Halesus radiatus, Polycentropus flavomaculatus* and *Agapetus fuscipes* were only found in cluster 1 streams. On the other hand, there are several species unique for cluster 2. They tend, however, not to be shared by many of the streams in this cluster. Examples of exclusive species for cluster 2 are *Velia caprai, Asellus aquaticus, Helodes minuta* and *Ilybius* sp. Other species, such as *Gammarus pulex, Ancylus fluviatilis* and baetid mayflies, were found to be widespread and did not contribute to the classification into clusters. In general, both grazers and shredders

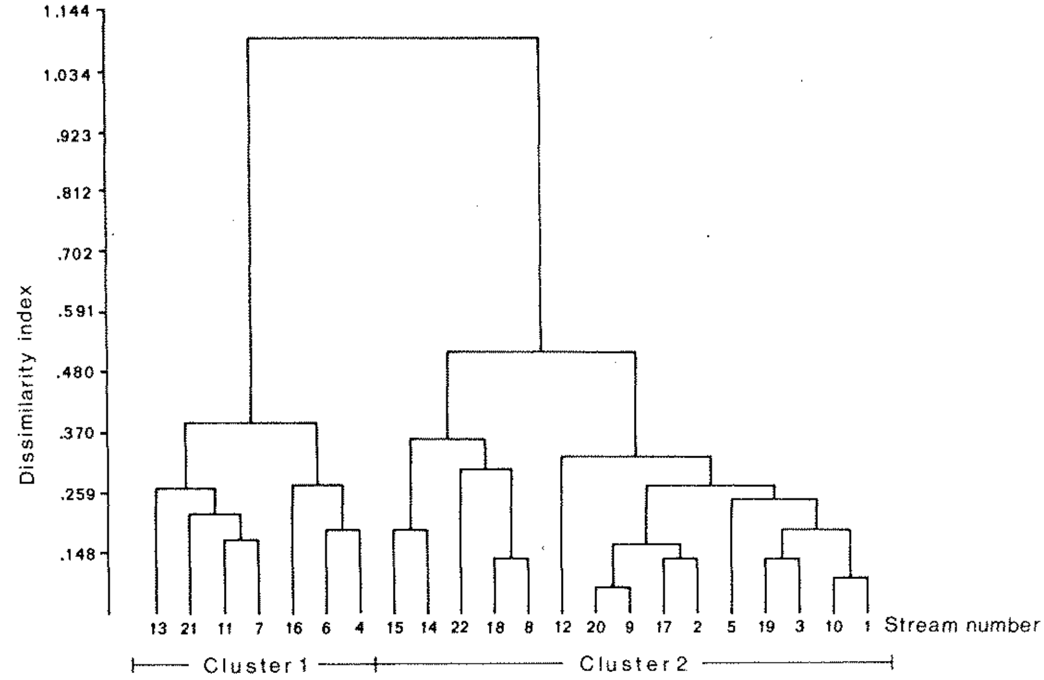

Fig. 3. Hierarchical clustering of the 22 study sites based on species composition.

were more common in cluster 1 than in cluster 2 (Chi-square = 4.98, $p < 0.05$ and Chi-square = 24.36, $p < 0.001$, respectively).

Some observations concerning abiotic factors are important in explaining the main clustering pattern. The average stream area for cluster 1 was significantly larger than that for cluster 2 (Mann-Whitney U-test, $p < 0.01$). Further, the streams in cluster 1 had a significantly ($p < 0.05$; Mann-Whitney U-test) lower conductivity than the streams of cluster 2 (53 ± 5.0 and 60 ± 7.4 mS m^{-1}, respectively, expressed as $\bar{X} \pm$ S.D). Also nitrate concentrations were lower in cluster 1 streams than those of cluster 2 (4.5 ± 2.1 and 6.2 ± 2.1 mg NO_3^- l^{-1}, respectively), although this difference was not significant (Mann-Whitney U-test, $p > 0.05$). To examine whether the faunal communities of clusters 1 and 2 differed with respect to species sensitive to organic pollution, the saprobic values of the streams of both clusters were compared. No significant differences was observed (Mann-Whitney U-test, $p > 0.05$).

Considering a lower level of similarity in the dendrogram (Fig. 3), four subclusters occurred, each from a dichotomy of clusters 1 and 2, respectively. In one of the subclusters in cluster 1, all streams have higher saprobic values than those of the other subcluster. Between the subclusters of cluster 2 there is a significant difference in the saprobic value (Mann-Whitney U-test, $p < 0.01$). Thus, the differences in water quality seem to be responsible for the subdivision of cluster 1 as well as cluster 2. Conversely, water quality differences did not seem to influence the grouping of streams into clusters 1 and 2, respectively.

Discussion

The slope (z) of the species–area relation of the 22 small streams was 0.19. For unionid mussels in 49 larger North American rivers Sepkoski & Rex (1974) obtained a value of 0.32. The different z-values of these running water studies may seem conflicting, since slopes of species–area relations in general tend to be steeper for small areas compared to large ones (cf. Lassen, 1975; Dony, 1977; Aho, 1978). In the streams investigated by us a majority of the animals were amphibiotic insects. Thus a high dispersal and immigration rate may be expected in animal communities of small streams in contrast to the mussel communities of the larger rivers. Further, the distance between the rivers studied by Sepkoski & Rex (1974) greatly exceeded those of our study. These factors may in part explain the low z-value of the Bornholm streams as compared to North American rivers.

Low z-values have also been documented in zooplankton communities (Nilsson & Nilsson, 1978; Browne, 1981). The diversity of zooplankton habitats does probably not increase concomitantly to the lake surface in contrast to that of shallow streams and rivers (Ulfstrand, 1967; Lowe-McConell, 1975). Thus, the low z-values might have entirely different explanations in these two types of communities.

The cluster analysis also indicated an effect of area on community structure. The two main clusters were found to differ significantly with respect to stream area. Both grazer and shredder species were more common in the large streams of cluster 1. Food availability to grazers was probably higher in the relatively unshaded large streams as compared to the small ones shaded by closed canopies (cf. Haefner & Wallace, 1981). This may be the reason why the grazers *Silo pallipes* and *Agapetus fuscipes* were present in cluster 1 streams but not in those of cluster 2. Shredders, feeding on leaves, also peaked in cluster 1 streams but here high food availability seems hard to accept as a factor ruling their distribution. One would rather expect that the availability and supply of leaf detritus would be greater per unit of area in the smaller streams (Naiman & Sedell, 1979; Otto, 1981). Nor did Hawkins *et al.* (1982) find shredders to be most abundant in streams with deciduous canopies. These observations indicate the categorization of feeding behaviour within this group to be inaccurate. Alternatively, in the present study food for shredders may have been more evenly distributed along the stream than expected from stream size.

Although stream size seemed to be the main factor governing the number of species present, nutrient load also affected the species distribution. In the two subclusters of streams with relatively lower conductivity and nitrate levels several species, such as *Baëtis rhodani, Rhyacophila fasciata, Elmis aenea* and *Scleroprocta* sp. occurred more frequently than in the more 'polluted' streams of the other two subclusters. *Erpobdella octoculata, Asellus aquaticus, Ilybius* sp., and tubificid worms on the other hand were more widely distributed among the polluted streams.

In conclusion, water quality affected the distribution of several species although stream size was the main factor explaining the number of species present. Stream size is no doubt in itself an abiotic factor, although it certainly has both biotic and abiotic implications. The increase in number of species with area is probably associated with an increase in the number of microhabitats. However, strictly biotic phenomena also increase in importance with increasing area. Such biotic factors as immigration rates and food diversity probably increase with area, whereas extinction rates decrease. To what extent these and other biotic factors such as competitive exclusion and keystone predation influence running water communities still remains to be assessed.

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