

Body Size Patterns in Stream Communities: A Test of Holling's Textural Discontinuity Hypothesis

Hamida BIBI^{1*} Dave RAFFAELLI² Mudassar IQBAL³
Muhammad SHARIF⁴ Muhammad Jammal Khan KHATTAK⁵

^{1,4,5}Department of Soil and Environment Sciences,
the University of Agriculture, Peshawar, PAKISTAN

²Departments of Environment, the University of York, UK

³Departments of Agricultural Chemistry, the University of Agriculture, Peshawar, PAKISTAN

*Correspondence author's email: drhamida@aup.edu.pk

ORCID IDs: ¹0000-0002-5955-6762, ²0000-0003-0132-9206, ³0000-0002-9339-7793,

⁴0000-0002-9214-4292, ⁵0000-0001-9345-8069

ABSTRACT

Theoretical studies of the resilience of ecological systems to environmental change predict that the size distributions of species in ecosystems should have discontinuities that reflect similar discontinuities in ecosystem processes. Body size distributions should have many peaks and troughs (modes) for natural, undisturbed ecosystems, but that as disturbances increases, so the number of modes declines. If so, this prediction has implications for assessing the quality of real ecological systems and has potential for environmental monitoring.

This paper explores the relationship between water quality and body size patterns in stream communities in order to establish the potential of size based indicators for assessing environmental conditions as well as testing Holling's (1992) proposition that lumpiness occurs in body size distributions across a broad range of spatial and temporal scales. Samples of the stream benthos were collected at different station in River Aire, Yorkshire, UK, which varies in water quality. All sites showed skewed distributions towards smaller size classes and most had two very obvious modes at medium and large size classes except for most polluted habitats. Analysis of the number of gaps using Holling's (1992) BMDI, revealed wide variation in clean and intermediate water quality sites, though the most polluted site had the fewest gaps. However other disturbed sites had more gaps and for some clean site had fewer gaps. It is clear that size distributions in stream communities are lumpy in the sense that most sites showed more than one mode or many gaps but the number of gaps (discontinuities) is not correlated with disturbances, at least for freshwater quality.

Key words: Size patterns, ecosystem resilience, benthic communities, water quality.

INTRODUCTION

Body size is an important parameter in ecological studies (Blackburn & Gaston, 1994), being a key determinant of a wide range of ecological and evolutionary parameters. Body size determines many aspects of life history such as metabolic efficiency, generation time and metabolism (Morse, Stork, & Lawton, 1988). The relationship between body size and abundance has been shown a useful tool for describing patterns across a wide range of taxa and habitats (Blackburn & Gaston, 1999) with a diversity of biotic and abiotic factors influencing these patterns (Maurer & Brown, 1988; Cyr, Peters, & Downing, 1997). Body size has strong potential to determine environmental impacts on community composition (Ptacnik, Moorthi, & Hillebr, 2010). The composition of small species due to relatively short generation time and high growth rate can quickly track the changes of local environment (Korhonen, Soininen, & Hillebrand, 2010). Departures from expected body mass distributions may provide an indication of disturbance in communities and insights into resilience (Damuth, 1992; Baho et al, 2015).

One approach to exploring body size and resilience has been developed by Holling (Holling, 1992). His Textural Discontinuity Hypothesis proposes that organisms develop specific physical and behavioural characteristics in response to the environmental texture which varies across scales and which is reflected in discontinuities in their body size distributions. In a wide range of marine ecosystems, the body size distribution of benthic organisms are tri-modal (Schwinghamer, 1988) and in planktonic systems biomass size spectra models indicate that size distributions are also multi-modal (Sheldon, Prakash, & Sutcliffe Jr, 1972; Thiebau & Dickie, 1992). The data from stony stream suggests that the body size distributions is dynamic and does not always falls into a single pattern (Stead, Jenny, Peter, & Alan, 2005) while bimodal size distribution was also reported across meio- to macrobenthos size range (Bett, 2013). Such discontinuities in the distributions of body size indicates self-organizing processes within ecosystems and may provide a tool to assess ecosystem resilience (Allen, Gunderson, & Johnson, 2005). These observations lead to the development of resilience theory and related concept, such as adaptive cycles of ecosystem processes operating at specific scales of space and time (Fig. 2) which consist of 4 phase: exploitation, conservation, release and re-organization.

There are multiple competing hypotheses regarding the determinants of body mass distributions of species. Community interactions (Hutchinson, 1959) and related ecological processes (Brown, Marquet, & Taper, 1993), the energetic hypothesis based on the allocation of energy for species growth and reproduction processes which are limited by the energy availability from the environment and by the subsequent transformation of energy into offspring (Marquet, Navarrete, & Castilla, 1995; Lovegrove & Haines, 2004; Allen et al, 2006); the phylogenetic hypothesis, reflecting different evolutionary histories of species (Cassey & Blackburn, 2004; Smith et al, 2004); the biogeographical hypothesis, which suggests that multiple modes in body size distributions are due to restricted set of species present in a given community (Silva, Brimacombe, & Downing, 2001). Many studies have found a relationship between body mass distributions and geographical range (Gaston & Blackburn, 1996; Pyron, 1999).

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An alternative explanation is the textural discontinuity hypothesis which argues that species respond to biotic and abiotic processes across different scales (micro, meso, and macro -scale) in time and space producing discontinuous distributions in their body sizes (Holling, 1992). The adaptive cycles operate at all spatial and temporal scale in a forest (Fig. 1). Many authors have argued that different landscapes and biomes with different ecological structures produce different patterns of body size distributions (Allen, Forsy, & Holling, 1999; Havlicek & Carpenter, 2001) and studies on freshwater fish found a relationship between gaps in body size distributions and habitat structure (Fu, Wu, Wang, Lei, & Chen, 2004). If the body mass pattern is controlled by landscape architecture, differences in phylogenetics, biogeography, energetics, and community interactions should not significantly change patterns in body mass configuration (Allen et al, 2006).

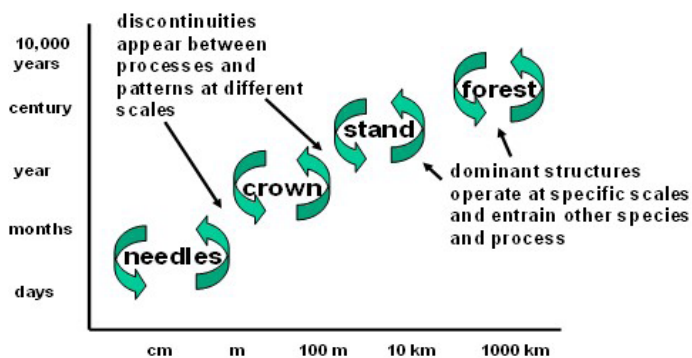


Fig. 1. Patchiness occurs at a range of spatial and temporal scales in nature, as shown in this example of a spruce forest ecosystem. In such systems, dominant structures (from needles to forests) operate over different spatio-temporal scales. The cycles of life and death for each of these structures may follow adaptive cycle dynamics (see Fig. 2), and these may entrain other ecological processes (Raffaelli & Frid, 2010).

Direct tests of these ideas are difficult but can be tested indirectly using surrogates of ecosystem processes, the body sizes of the organisms in the ecosystem; because body sizes are a reflection of processes operating at different scales. Thus, in Holling's plots of the adult body sizes of birds and mammal species from North American grasslands and forests, many modes are apparent which he claimed were associated with ecosystem processes operating at specific scales (although the identities of these processes were not known, only suspected). The regions between modes, the so-called "gaps", were claimed to represent the discontinuities between ecosystem processes. Holling further argues that these gap regions would be the most susceptible to disturbance and where species losses would be most likely. These ideas were further tested by examining how the body sizes of invasive species in the Florida Everglades (Allen et al, 1999) and elsewhere fitted in to the existing body size distributions of the community being invaded, reviewed in (Allen et al, 2006) and references therein. The study found that invasive species tended to have body sizes that were immediately adjacent to the gap regions, and that species which were lost due to disturbance were close to these gaps, consistent with Holling's predictions.

(Raffaelli, Hall, Emes, & Manly, 2000) also tested this idea for a marine intertidal community and found that the body size distributions were multimodal as suggested by Schwinghamer (Schwinghamer, 1981b) for marine sediments and that at least one kind of disturbance, which were applied experimentally, organic enrichment, had the greatest impact on body sizes in and adjacent to one the troughs between modes.

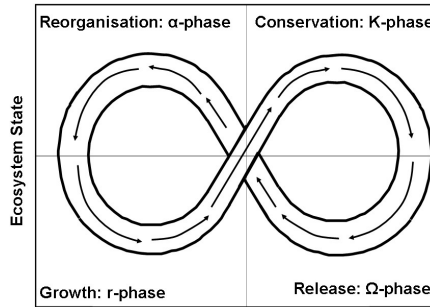


Fig. 2. The adaptive cycle view of ecosystem development and change. In this perspective, collapse of the system is inevitable, whereupon the system components may re-assort and begin development again as a broadly similar system or one which is very different (Raffaelli & Frid, 2010).

From the above, it can be seen that one of the effects of disturbance on body size distributions may be first to deepen the troughs between modes (make them more pronounced), if that disturbance only leads to species loss, as in the case of eutrophication (Fig. 3). However, the response of ecological systems to eutrophication or enrichment is not usually a “simple, or monotonic”. At moderate enrichment, there may be an increase in the abundance of all species (and body sizes), but at higher levels of enrichment, the positive effects may be overtaken by the negative effects as some species intolerant of low oxygen concentrations brought about by a high BOD may be excluded and smaller taxa which are more tolerant of pollution dominate. In such cases, the body size distributions may at first maintain their structure and modality, but as pollution increases, the larger taxa will become excluded and the size structure becomes more skewed towards smaller animals altering modality. Such changes in body size distributions are well-documented in aquatic communities as empirical observations (Warwick, 1984), but their consequences for, and relationships with, changes in ecosystem processes at different scales have not been explored in the context of Holling’s theories.

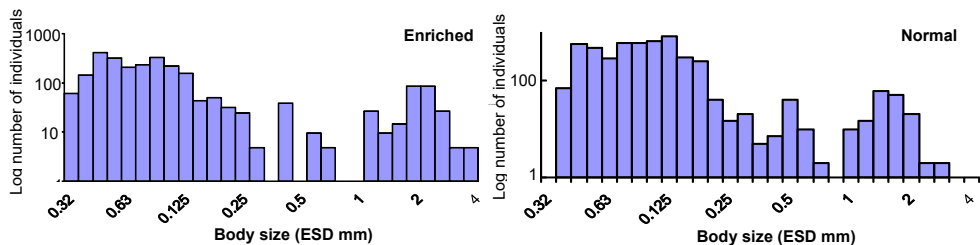


Fig. 3. The effect of pollution on body mass distributions on benthic communities (Raffaelli et al, 2000).

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As far there have been no previous experimental or empirical published studies looking at the degree of modality in body size distributions (as a reflection of the heterogeneity in ecosystem processes) and disturbance (in this case pollution). A similar loss of larger body size modes (reduction in modality) can be seen in comparisons of the Pleistocene fauna of North America with the present day, due to over-exploitation of the megafauna by early man (Smith et al, 2004), but that research was not placed in the context of Holling's hypothesis. This paper therefore represents the first empirical test of this aspect of Holling's theory.

In this paper the hypotheses regarding body size distributions in relation to the stability /stress of freshwater stream communities have been explored. Specific objectives of the paper included;

- Establish the modality of benthic body size distributions across a gradient of environmental stress (sites with differing water quality).
- Explore the relationship between the number of gaps in body size distributions and water quality using a gap finding approach proposed by Holling (1992).
- Assess whether the modality and number of gaps has potential for assessing the ecological health (resilience) of streams.

METHODS

Samples of benthic invertebrates were taken from sites along the River Aire, North Yorkshire in September and October of 2008 and 2009. The sites were pre- selected according to their water quality previously determined by the Environment Agency UK (Table 1). The RIVPACS data was provided by environmental Agency for most of the sites (Table 4). At each site, 5 repeat Surber samples (0.25m² base area, 200µm net) were taken to allow collection to be dispersed over a wide spatial extent. The fauna collected was preserved in ethanol, identified to the lowest taxonomic level and the body size (mass) of all individuals estimated from morphometric- based formulae (Table 3) or, for larger individuals, by water displacement. Water quality was also assessed using invertebrate samples as the biotic index Average Score Per Taxon (Mason, 2002a).

Table 1. Sites sampled on the River Aire and their general grade as assessed by environment agency.

	Sites	General water quality
1	Winterburn	Very good
2	Airton	Very good
3	Otterburn	Good
4	Hetton	Good
5	Gargrave	Fair
6	Carlton bridge	Fair
7	Esholt village	Fairly good
8	Calverley bridge	Poor
9	Thwaites mill	Bad

Body size distributions were plotted for each site in order to evaluate the degree of modality. In addition, individuals (and taxa) were ranked in increasing body size and the body mass difference index (BMDI) calculated between consecutive rankings using Holling's (1992) formula:

$$\text{BMDI} = (M_{n+1} - M_{n-1}) / (M_n)^y$$

Where M_n is the body mass of n^{th} species in a rank order of increasing size and y is exponent sufficient which values 1.1 as the invertebrates exploit their resources with dimension 1, i.e, finding a path of a certain width. The mean BMDI was calculated as well as the mean +2SE criterion line in order to estimate the number of significant gaps in the distributions. Two consecutive differences values above the mean +2SE; followed by four value below the line is a considered conservative and robust method to detect gaps (Holling, 1992).

RESULTS

The water quality at the site, as determined from the ASPT estimates, was broadly similar to the classification provided by Environment Agency. Winterburn was cleanest on the ASPT range and Thwaites mill and Calverly bridge had the poorest water quality (Fig. 5). The fauna found at each of these sites is shown in Table 2, Fig. 4. Winterburn was dominated by stoneflies (Leuctridae and Perlodidae), Haliplidae, Chironomidae and Simuliidae. In Airton large number of Haliplidae, Chironomidae, Gyrinidae, Diptera and Oligochaeta was recorded. Otterburn had many Haliplidae, Gyrinidae, Chironomidae, Diptera and Oligochaeta. The dominant taxa in Hetton were Haliplidae Baetidae, Chiromidae, Oligochaeta and Diptera, while in Gargrave high abundances of Chironomidae, Dixidae, Haliplidae, Oligochaeta and Diptera was recorded. In Carlton bridge the dominant taxa were Nematomorpha, Chironomidae, Oligochaeta, Haliplidae and Baetidae. The most abundant species in Esholt village are Oligochaeta, Chironomidae, Hydrosychidae, Asellidae, and Nematomorpha. Calverly bridge was dominated by Oligochaeta, Chironomidae, Hydropsychidae, Nematomorpha and Asellidae. The site with poor water quality Thwaites mill had abundant Oligochaeta, Chironomidae, Asellidae, Hydrodiidae and Viviparidae. Thus our analyses confirm a gradient of water quality in the River Aire at these sites.

Table 2. Community abundance of River Aire, showing the numbers of each fauna present at each sites.

Taxa	Winterburn	Airton	Otterburn	Hetton	Gargrave	Carlton bridge	Esholt village	Calverly bridge	Thwaites mill
Baetidae	7	37	21	53	20	15	50	40	1
Ephemerillidae	61	17	1	5		2	15	10	
Heptagonidae				2	2	1	28	13	
Potamintidae				1	5				
Leuctridae	400	41	18	10		2			
Perlodidae	90			5	1		1		
Haliplidae (L)	131	295	545	75	73	57	4		

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Table 2. Continued.

Taxa	Winterburn	Airton	Otterburn	Hetton	Gargrave	Carlton bridge	Esholt village	Calverley bridge	Thwaites mill
Diptera	29	53	123	16	21	10	7		
Oligocheata	12	48	76	43	37	62	700	771	92
Nematomorpha						68	104	104	
Tipulidae	1	8	20	1		1	8	7	
Chironomidae	127	65	132	52	487	63	632	375	30
Halipilidae (A)				1					
Gyrinidae	7	55	151	1	13	5	2		
Dytiscidae	9	6	4			1		2	
Trichoptera		29	11	4	1		9		
Hydropsychidae	34		23	6	10	9	153	110	1
Rhyacophilidae	6					3			
Ceratopogonidae			2	1		6	1		
Simuliidae	44	12		1		2	1	1	
Dixidae	4	10	19		91	5	21	7	
Gammaridae	1	19			3		2		
Glossiphoniidae	1	1	6		1	5	60	19	
Erpobdellidae			9					3	
Hymenoptera				7					
Hydracarina									
Sphaeriidae							3		
Viviparidae		4							2
Valvatidae									1
Hydrobiidae		3	26						2
Asellidae							132	53	7
Arachnida		1	3				1		
Hemiptera		1					2		
Hydrometridae		1						2	
Chalcididae	1	3				4	2	6	
Cladocera		7	9						
Veliidae	1								
Polycentropodidae	32	2							
Planorbidae	1								
Ecdyonuridae		1	1						
Ancylidae	1	2							

Table 3. Regression equations for body mass determination of Stream communities where DM is the dry mass of the organism (mg), DW is dry weight (mg) of the organism, L is the length of the organisms (mm), HW is head width of the organism (mm), volume (V) of the organisms expressed in (nL), Wt is weight of the organisms (mg).

Family/Class	Regression equation to determine body mass of fresh water invertebrates	References
Baetidae Heptageniidae Caenidae Ephemereillidae Ephemeridae Potamanthidae Hymenoptera Ecdyonuridae	$Dw(mg)=aL(mm)^p$ $Dw(mg)=3.8 \times 10^{-3} L(mm)^{2.918}$	(Stead et al, 2003) and reference within
Diptera	$DM(mg)=aL(mm)^p$ $DM(mg)=1.3 \times 10^{-3} L(mm)^{2.851}$	
Leuctriodae Perlodidae	$Dw(mg)=aL(mm)^p$ $DW(mg)=2.5 \times 10^{-3} L(mm)^{2.744}$	
Gammaridae	$\ln DM(mg)=\ln a + b \ln L(mm)$ $\ln DM(mg)=-4.95 + 2.83 \ln L(mm)$	
Tipulidae	$DW(mg)=aL(mm)^{2.851}$ $Dw(mg)=1.3 \times 10^{-3} L(mm)^{2.851}$	
Chironomidae Caratopogonidae	$DM(mg)=a L(mm)^p$ $DM(mg)=6.0 \times 10^{-4} L(mm)^{2.770}$	
Hemerobiidae	$\log DM(\mu g)=a+b \log HW(mm)$ $\log DM(\mu g)=2.68+2.9 \log Hw(mm)$	
Trichoptera Rhyacophiliidae Hydropsychidae	$\ln DM(mg)=\ln a+b \ln L(mm)$ $\ln DM(mg)=-6.037+2.82 \ln L(mm)$	
Simuliidae	$\ln DM(mg)=\ln a+b \ln Hw(mm)$ $\ln DM(mg)=-4.5009+2.0742 \ln Hw(mm)$	
Arachnida Argulidae	$DM(\mu g)=aL(\mu m)^p$ $DM(\mu g)=1.1 \times 10^{-6} L(\mu m)^{1.89}$	
Oligochaeta	$DM(nl)=a L(\mu m)^p$ $DM(nl)=3.5 \times 10^{-3} L(\mu m)^{2.1}$	
Dixidae	$DM(mg)=aL(\mu m)^p$ $DM(mg)=6.62 \times 10^{-4} L(\mu m)^{2.59}$	
Cladocera	$\ln DM(\mu g)=\ln a+b \ln L(mm)$ $\ln DM(\mu g)=\ln 1.7512+2.653L(mm)$	
Asellidae	$DM(mg)=aL(mm)^p$ $DM(mg)=7.2 \times 10^{-3} L(mm)^{2.785}$	
Nematomorpha	$DM(\mu g)=a L(\mu m)^p$ $DM(\mu g)=6.0 \times 10^{-5} L(\mu m)^{0.8205}$	
Turbullaria	$V(nL)=L(mm) \times W^2(mm) \times C$ $V(nL)=L(mm)W^2(mm) \times 550$ $V(nL) \times 1.05 = \text{dry weight} = \mu g$ $\mu g/1000=mg$	
Piscicolidae Erpobdellidae Glossiphoniidae	$V(nL)=L(mm) \times \pi(W/2)^2 \times 530$ $V(nL) \times 1.13 = \text{dry wight}(\mu g)$	(Leaper et al, 2001)
Valvatidae Unionidae Planorbidae	Water Displacement $V(nL)=WD(\mu L) \times 1000$ $Wt(\mu g)=v(nL) \times 1.05$ $Mass(mg)=\mu g/1000$	
Hydrobiidae Physidae Viviparidae	$V(\mu L)=L(mm) (0.851)^{1.91}$ $Wt(\mu g)=v(\mu L) \times 1.05$ $Mass(mg) = \mu g/1000$	
Ancylidae Sphaeriidae	Approximate a geometric shape (cone) $V(\mu L)=1/3\pi r^2 (mm) h(mm)$ $V(nL)=\mu L \times 1000$ $Wt(\mu g) = nL \times 1.05$ $Mass (mg) = \mu g/1000$	

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Table 3. Continued.

Family/Class	Regression equation to determine body mass of fresh water invertebrates	References
Corixidae Notonectidae Mesoveliidae Veliidae Hydrometridae Hemiptera	$\ln W(\text{mg}) = \ln a + b \ln L$ $\ln W(\text{mg}) = -4.200 + 2.60 \ln L(\text{mm})$	(Smock, 1980)
Gyrinida Dyticidae Halplidae	$Dw(\text{mg}) = \ln a + b \ln L(\text{BL}(\text{mm}) \text{ or } HW(\text{mm}))$ $Dw = -2.0076 + 3.2271 \ln L(\text{BL} - Dw)$ $Dw = 3.1102 + 2.5412 \ln L(HW - DW)$ converted BL to HW by using $HW:BL$	(Tower et al, 1994)

Habitats at the sites

There are six categories of general quality assessment (GQA) of water: very good, good, fairly good, fair, poor and bad. These classes have been determined by the Environment Agency in England, by combining two parameters, an ecological quality index based on the ASPT measure described above and the taxa present in the water body (Mason, 2002b). The computer model, RIVPACS (River Invertebrates Prediction and Classification System), has been developed to assess environmental stress based on the physical, geographical and chemical characteristics of a site, and what the invertebrate fauna of that site would look like in the absence of pollution. A comparison of the predicted macroinvertebrates communities with those actually observed allows calculation of ecological quality indices (EQI). The most relevant EQIs in describing biological quality are based on the number of macroinvertebrate taxa and ASPT as follows:

EQI taxa = Observed number of taxa present on given habitat (Predicted from RIVPACS)

EQI ASPT = Observed ASPT for the present taxa on given habitat (Predicted from RIVPACS)

RIVPACS habitat data for the different sites on the River Aire were supplied by the Environment Agency and the most relevant variables are shown in Table 4. These data show that all the sites are stony shallow riffles which do not differ greatly in their substrate composition. Any between-site differences in BMWP and body size distributions are thus unlikely to be due to differences in stream bed characteristics or to bank vegetation as indicated by the shading score.

The RIVPACS data sheets also provide information on conductivity, related to dissolved solids and suspended material and general chemical characteristics of natural water (Hem, 1985). Significant changes in water conductivity could indicate pollution, pure (low conductivity) water being a good conductor of electric current. Thus, a positive relation has been found between pollution levels and conductivity (Ali, Ahmed, Othman, & Othman, 2009). In the present study, conductivity values were available for most sites on the Aire (Table 4) and there is a clear relationship between conductivity and water quality (ASPT) (Fig. 9).

Table 4. RIVPACS data for different sites on River Aire provided environmental agency leads.

Winterburn	Light	Slight	None	8	20	208	None	Unstable	5	65	15	5	5	0	Yes
Hetton	Moderate	Slight	None	6.2	20	275	None	Stable	10	60	15	10	5	0	Yes
Gargrave	None	Clear	None	25	25	355	None	Stable	5	60	20	10	5	0	Yes
Carlton Bridge	None	Clear	None	14	20	283	None	Unstable	0	40	40	10	10	0	Yes
Esholt Village	Light	Slight	None	15	40	381	None	Unstable	0	70	30	0	0	0	Yes
Calverley Bridge	None	Clear	None	35	30	664	None	Unstable	5	45	40	5	5	0	Yes
Thwaites Mill	None	Clear	None	20	60	348	None	Stable	5	55	30	0	10	0	Yes

The body size distributions of benthic fauna at the sites are shown in Fig. 6. The data here are shown on a linear body mass scale (0.25-5 mg), but the shape is similar across a range of bin sizes and transformations. All sites show a skewed distribution towards smaller size classes and none of the sites can be adequately described by a single uni-modal distribution. In addition to the left-skewed mode, there is often a clear mode around 1-2 mg and possibly another mode in the largest size classes, although neither are apparent for Thwaites mill.

In contrast to left-skewed distributions, analysis by Kernel Density Estimate (KDE) revealed multiple modes for the most clean site Winterburn (Fig. 7, Table 5), and a single mode for the most polluted site (Thwaites Mill). However there was no consistency in the number of modes in body size spectra for intermediate quality water sites. The sites which are considered cleaner often had fewer modes while less clean sites had more modes. Thus, the number of modes for intermediate quality water are more variable, but all sites present at least bimodality, except for the most polluted habitat.

Analysis of the number of gaps, following Holling's methods, shows wide variation in the number of body size gaps detected (Fig. 8). The highest numbers of gaps occurred at the Esholt site which has moderate water quality and the lowest number of gaps was recorded in Carlton bridge having a fair water quality according to the Environment Agency and ASPT analysis. Consequently, there is no clear relationship between the number of gaps and water quality (Fig. 10, $R^2 = 0.0014$, $p > 0.5$).

Table 5. Results of the test of significance for the sites spectra from the kernel density estimation and smoothed bootstrap re-sampling where h is smoothing constant used in kernel estimation, m is the smallest number of modes for which the bootstrap test was not significant at the 5% level, P level of significance for each distribution (mode number).

Sites	h	m	p	Sites	h	m	p
Winterburn	0.126	3	0.496	Carlton Bridge	0.353	2	0.103
Airton	0.178	2	0.292	Esholt Village	0.128	3	0.467
Otterburn	0.47	2	0.23	Thwaites mill	0.153	1	0.802
Hetton	0.173	2	0.338	Calverly Bridge	0.194	3	0.055
Gargrave	0.137	4	0.095				

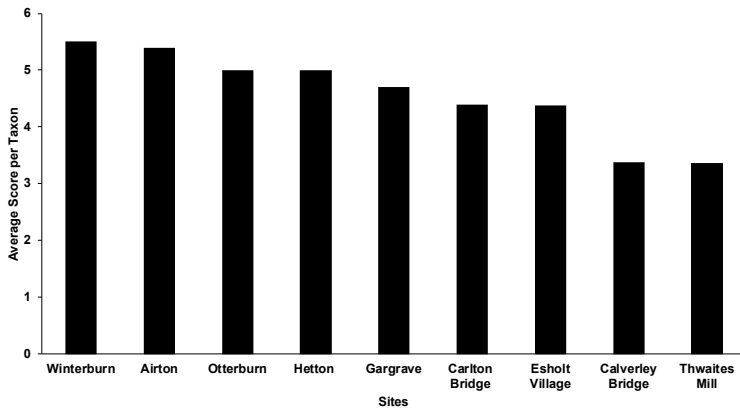


Fig. 2. Average score per taxon for different sites on the river Aire, varying in water quality. The score declines with decreasing water quality.

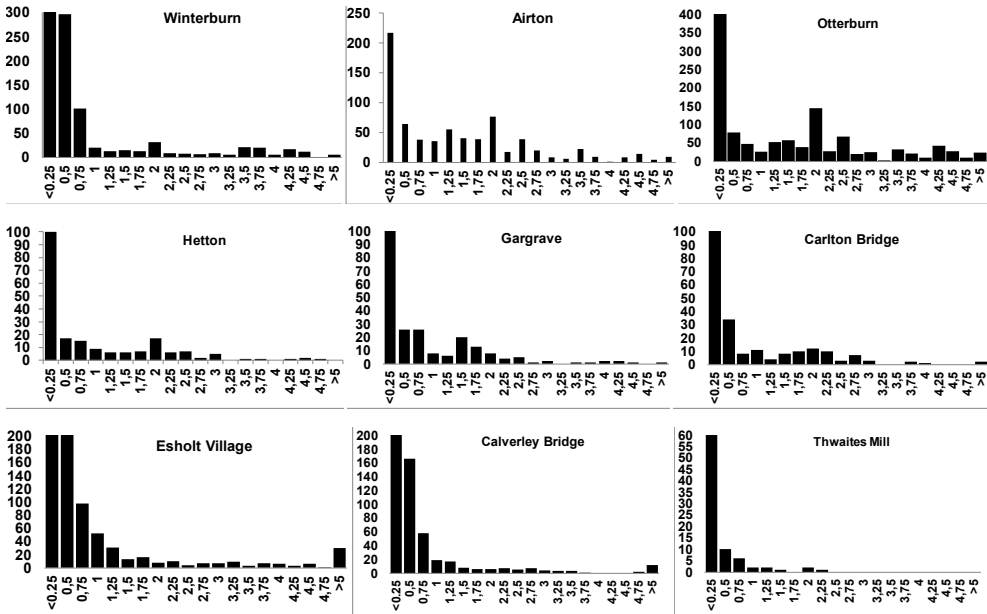


Fig. 3. Body size distribution for invertebrates of river Aire flows from Winterburn to Thwaites mill. Body mass were measured in mg, ranging from <0.02 to >5, plotted at x-axis while number of individuals are shown at y-axis. The distribution of body masses presents multimodality several sit.

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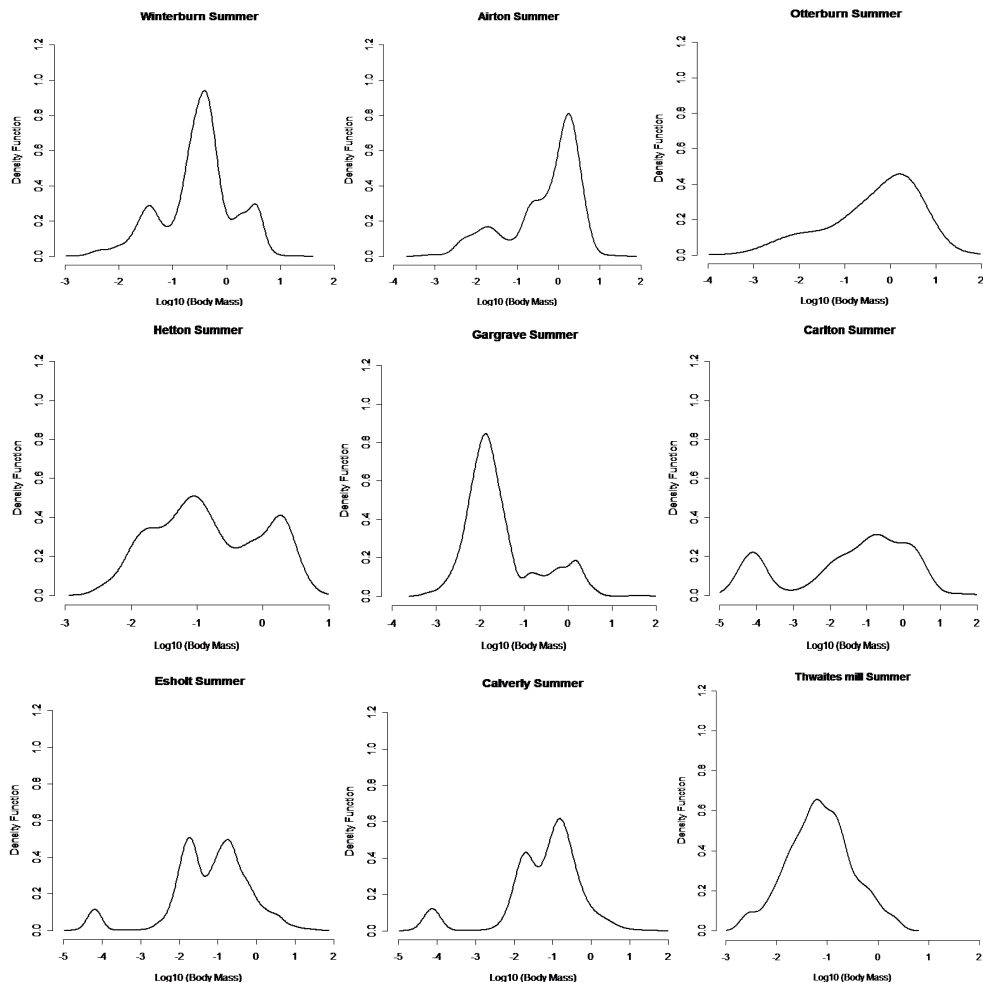


Fig. 4. The fitted distributions for density-body size estimated by Kernel density estimation and bootstrapped re-sampling at river Aire. Both axes are scaled as log to base 10 of the original data. Density function=number of individuals per core.

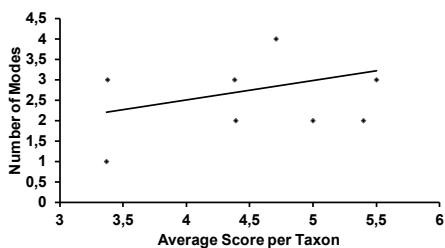
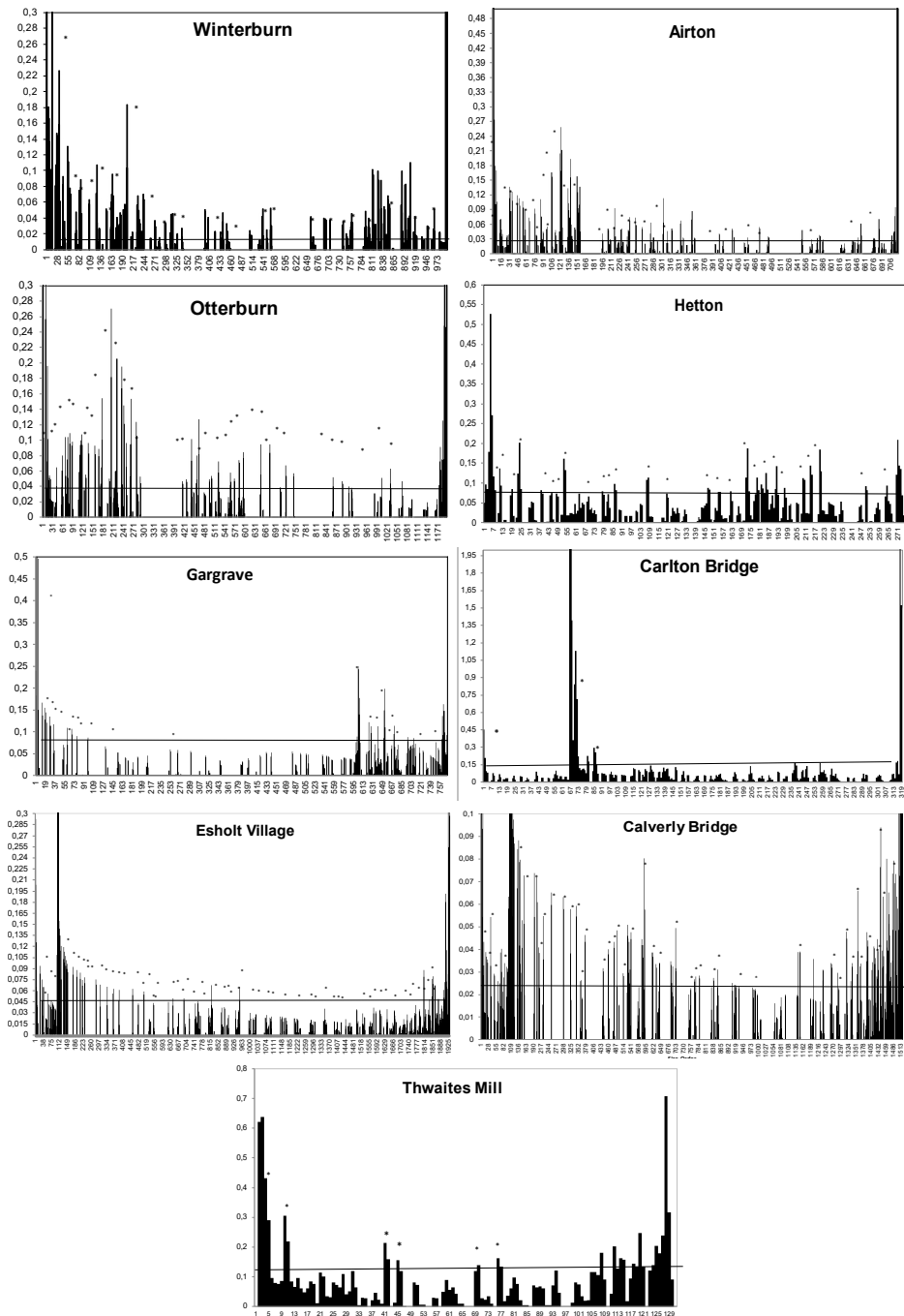


Fig. 5. The relationships between water qualities determined by biotic index (ASPT) and number of body mass modes determined by Kernel density estimates.



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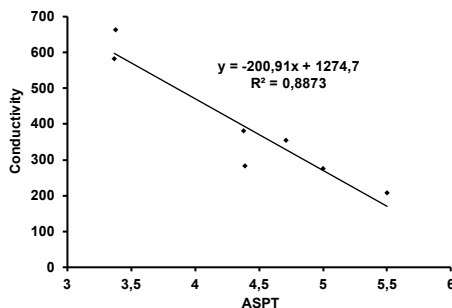


Fig. 7. The relationship between water quality (ASPT) and water conductivity.

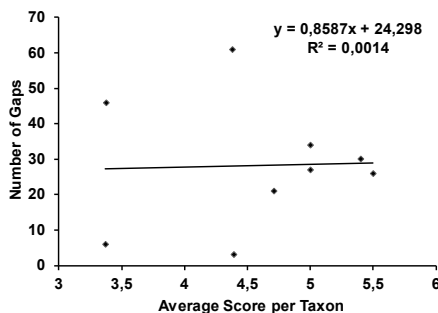


Fig. 8. The relationship between the number of gaps and average score per taxon for different sites on the river Aire. The vertical arrow indicates the number of gaps detected in body mass distributions.

DISCUSSION

The study was carried out to assess the effects of water quality on body mass distributions in stream communities. Benthic fauna were sampled across different site on the River Aire varying in water quality, to establish the potential of size based indicators for assessing environmental condition. Water quality had been classified by the Environment Agency UK and also assessed by us using invertebrate samples as the Average Score per Taxon (Mason, 2002). The ASPT estimates for the sites were similar to the classification provided by Environment Agency. The highest score of 5.5 was for the cleanest site and scores decreases with decreased water quality with the lowest score of 3.37 for the most polluted sites as reported in another studies of reducing score of the index with decreasing the quality of water (Ariella & Atiek, 2017).

The analysis of the size distributions showed that most sites were clearly not unimodal with respect to their body size distributions as claimed by many authors that body mass distributions in communities are multimodal (Schwinghmer, 1981a; Poff et al, 1993; Matthews, Borges, & Whittaker, 2014), although some do show uni-modal size spectra (Solimini, Benvenuti, D'Olimpio, Cicco, & Carchini, 2001). In the River Aire, body size distributions showed at least bimodality for invertebrates, mainly in the cleaner sites which supported a wide range of body sizes. The most polluted sites

(Calverly bridge and Thwaites mill) were better described as unimodal. There were a large number of small size individuals within these sites.

Whilst the above presents some evidence for changes in modality with water quality, this was not reflected in the BMDI analysis. For gap analysis, more discontinuities (body size gaps) imply less disturbed communities (Holling, 1992), but in our study there was no relationship between number of gaps and water quality as measured by ASPT. Many gaps were observed at Esholt village which had a fairly good quality compared to the cleaner site (Winterburn). 61 gaps were recorded in Esholt village followed by Calverly bridge with 46 gaps. Otterburn, Airton and Hetton are good quality habitats but in our gap analysis these sites revealed 34, 30 and 27 gaps, respectively. At the cleanest site (Winterburn), the number of gaps was 26 while in Gargrave 21 gaps were recorded. One of the lowest numbers was recorded in the polluted site (Thwaites mill) with 6 gaps, but in contrast a fair quality habitat (Carlton bridge) had only 3 gaps. Thus, there was no clear relationship between ASPT and the number of gaps. Finding gaps using the BMDI approach seems to be sensitive to the presence of exceptionally large values of BMDI that increase the mean value hugely making it almost impossible to detect the gaps which occur amongst the lower BMDI values.

In this research work the leading competing hypotheses were categorized which explaining body size distributions in ecosystems. The scale varies for each hypothesis and there is no evidence that one scale is superior to other scales of analysis (Vermaat, Eppink, van den Bergh, Barendregt, & van Belle, 2005) because different processes are important at different scales, and so no single theory can explain the patterns across different scales (Gaston, Chown, & Mercer, 2001). To link the body mass patterns to the processes affecting those patterns, multiscale analysis is critical (Krawchuk & Taylor, 2003), but there is evidence of multimodality (Havlicek & Carpenter, 2001) and discontinuity in body mass distribution in a range of ecosystems (Allen et al, 1999). The present study compares adjacent systems with different environmental conditions, so that the taxonomic identities of species and their evolutionary histories will be similar, thus phylogenetics are held constant. The system is spatially connected and allows species to disperse across the habitats which varies from clean to pollute and existence of body mass patterns cannot be due to biogeographical separation. The community interaction hypothesis predicts that changes in the patterns of body size are because of different taxa present in the system, but such taxonomic differences are restricted to the species level, not the higher-level taxa dealt with here. The textural discontinuity hypothesis predicts changes in body size patterns because the habitat available to the animals differs. The presence of multiple modes and gaps in cleaner sites reflects the hierarchical physical structure of the system and shows that multiple processes are responsible to structure a dynamic ecosystem. At the most polluted sites (Thwaites mill), fewer modes might be a sign of a disturbed and less resilient system, although the number of gaps for other polluted sites is higher and for some clean site is lower.

In conclusion, it is clear that body size distributions in stream communities are “lumpy”, in the sense that most site shows more than one mode or many gaps. The

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most polluted site in our study had the fewer modes and gaps and the cleanest site had many gaps and were clearly multimodal. In term of Holling's (1992) textural discontinuity hypothesis, these patterns could reflect the dynamic processes operating at particular scales, no other competing hypotheses seeming plausible. However, it is also clear that the number of gaps (discontinuities) is not well correlated with disturbance, at least water quality, but further empirical exploration of such relationships is needed given their compelling theoretical basis (Holling, 1992).

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