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Statistical quantification of the effect of thermal stratification on patterns of dispersion in a freshwater zooplankton community

Stephen J. Thackeray[1],*, D. Glen George[1], Roger I. Jones[2] and Ian J. Winfield[1]
*[1]Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, UK; [2]Department of Biological and Environmental Science, University of Jyväskylä, PL 35, 40014, Jyväskylän Yliopisto, Finland; *Author for correspondence (e-mail: sjtr@ceh.ac.uk; fax: +00-44-(0)-1524-61536)*

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Abstract

The vertical distribution of crustacean zooplankton species was examined during 2000 in Windermere, Cumbria. Patterns of dispersion were evaluated quantitatively using two different approaches. Firstly, Morisita's index was used to test whether patterns of dispersion differed significantly from a state of randomness and, secondly, the relative distribution of zooplankton individuals between the epilimnion and hypolimnion was investigated, for a series of standardised vertical profiles of organism density. All six of the dominant species of planktonic crustaceans showed aggregated patterns of dispersion throughout the year. For most species, patterns of dispersion were affected by the onset and breakdown of thermal stratification in the lake. The degree of aggregation in the vertical plane, measured using Morisita's index, increased when the lake became thermally stratified. Furthermore, for most species, there was a positive association between the degree of vertical differentiation in abundance across the thermocline, and the degree of temperature differentiation in the stratified water column. The results of the present analysis provide quantitative evidence for the phenomenon known as 'zooplankton stratification' and for temporal variation in patterns of zooplankton dispersion.

Introduction

In nature, organisms are rarely randomly distributed (Taylor 1961; Elliott 1977) and are most often aggregated in space (Taylor et al. 1978). Furthermore, some incidences of apparent randomness in spatial distribution merely reflect an inability to detect heterogeneity statistically, due to the low densities of organisms in the study site, a state of 'pseudo-randomness' (Taylor 1984). Spatial heterogeneity is a reflection of patterns of individual behaviour and of demographic changes (Taylor and Taylor 1977; Anderson et al. 1982; Taylor 1983; Elliott 2002) and is functional in ecosystems, having the potential to influence population dynamics and community level interactions (Dutilleul and Legendre 1993).

Populations of crustacean zooplankton are frequently characterised by such heterogeneity, as the individual organisms that comprise them respond to spatial structure in the abiotic and biotic environments. In temperate lakes, thermal stratification is a major determinant of such environmental structure. During the stratified period, patterns of vertical mixing interact with physical, chemical and biological processes, inducing spatial heterogeneity in dissolved oxygen concentrations, food resources and the abundance of potential predators and competitors (Ruttner 1953). As a result of the responses of individual organisms to such environmental heterogeneity, populations and communities of planktonic organisms frequently become heterogeneous under conditions of thermal stratification. At this time zooplankton are known to associate with thermal structures (Burns and Mitchell 1980; Marcogliese and Esch 1992) and the degree of spatial heterogeneity appears to be partially dependent on the intensity of physical structuring (Hofmann 1975; Miracle 1977). This progressive increase in the degree of zooplankton spatial heterogeneity in response to thermal stratification has been termed 'zooplankton stratification.'

Previous investigations of vertical structure in freshwater planktonic communities have frequently been subjective, adopting a descriptive approach to the analysis of spatial pattern and its relationship to environmental structure (Muller 1985; Matsumura-Tundisi 1997). Typically the evidence for zooplankton stratification in freshwater systems has only been evaluated qualitatively, after visual inspection of vertically resolved thermal and biological data. The objectives of the present study were: (1) to quantify statistically the patterns of dispersion for the dominant crustacean zooplankton taxa in a stratifying freshwater lake; and (2) to investigate whether patterns of dispersion were modified in response to changes in thermal stratification. More specifically we tested the hypotheses that: (1) zooplankton populations will become more aggregated with an increase in water column thermal differentiation; and that (2) during the stratified period the difference in zooplankton abundance across the thermocline will become more pronounced with an increase in water column thermal differentiation.

Materials and methods

Collection of field data

Crustacean zooplankton were sampled over the deepest point (64 m) of the north basin of Windermere, Cumbria, UK (54°20′ N, 2°57′ W) using a messenger-activated closing net (mesh size = 160 μm, mouth diameter = 250 mm) to collect samples from a series of twelve 5 m deep strata covering the 0–60 m depth range. Samples were preserved in a 4% solution of formaldehyde, prior to microscopic enumeration and identification according to the keys of Scourfield and Harding (1966) and Harding and Smith (1974). Samples were collected at approximately 2 week intervals between late April and late December 2000, and were always collected between 10:00 and 11:00 h. The vertical temperature profile was also recorded on each date in order to provide information on the physical structure of the water column. Given that the temperature profile reflects the physical structuring of the water column, and that thermal stratification frequently permits spatial heterogeneity in a multitude of biologically relevant variables, we use these temperature measurements as a proxy for total environmental structure.

Statistical methods

Patterns of dispersion were investigated for each zooplankton species using an established single-sample index of dispersion. Morisita's index was chosen, as it is independent of both the sample mean and the total number of organisms found in the sample (Elliott 1977). The index was calculated as:

$$I_\delta = n \cdot \left(\sum(x^2) - \sum x\right) / \left(\left(\sum x\right)^2 - \sum x\right) \tag{1}$$

where x is the number of individuals in a given sampling unit and n is the number of sampling units. The index is equal to 1 for a random distribution, less than this for a regular distribution and greater than 1 for an aggregated distribution. For each species, on each sampling date, departures from randomness were tested according to Elliott (1977).

In order to test the hypothesis that zooplankton populations will become more aggregated with an increase in the degree of thermal differentiation in the water column, values of Morista's index were correlated with a variable chosen to represent the degree of physical water column structure on a given date. The chosen variable was the water column temperature difference, hereafter WCTD (the maximum water temperature in a given depth profile minus the minimum temperature). All associations were tested using the Spearman's rank correlation method.

Although useful for quantifying the degree of aggregation in biological populations, dispersion indices do not provide any information on where exactly samples have been taken and, therefore, cannot elucidate the part of the habitat under study in which organisms are found. For this reason, the dispersion analyses in the present study were complemented by an analysis of the vertical differentiation in zooplankton abundance relative to the position of the thermocline on each sampling date. On each date, thermocline depth was defined as the depth of the maximum temperature gradient. The period of thermal stratification was defined as the period over which the recorded maximum temperature gradient exceeded 1 °C m^{-1} (Lampert and Sommer 1997). During the stratified period the proportion of each zooplankton population that was found above the thermocline was calculated and differenced from the proportion that was found below the thermocline. To test the hypothesis that, during the stratified period, the difference in zooplankton abundance across the thermocline will become more pronounced with an increase in water column thermal differentiation this difference was then correlated with the WCTD using the Spearman's rank correlation method.

Results

The pelagic crustacean zooplankton community of Windermere was dominated by only six species. These comprised two cladocerans (*Daphnia galeata* Sars and *Bosmina obtusirostris* Sars), two calanoid copepods (*Eudiaptomus gracilis* Sars and *Diaptomus laticeps* Sars) and two cyclopoid copepods (*Cyclops strenuus abyssorum* Sars and *Mesocyclops leuckarti* Claus).

Visual inspection of vertical distribution patterns indicated that changes in dispersion were coincident with changes in thermal stratification. Illustrative examples of this qualitative interpretation, are given in Figure 1. Prior to the establishment of a stable thermocline, the cladoceran *Daphnia galeata* was found to be dispersed throughout the upper 20 m of the water column (Figure 1). However, when thermal stratification became pronounced, this species became more restricted in its vertical distribution, primarily inhabiting the upper 10 m of the water column. Although, visual inspection of the data suggests that this organism was vertically patchy on both occasions, the degree of patchiness appeared to have increased after thermal stratification. It also appeared that the dispersion pattern of the calanoid copepod *Eudiaptomus gracilis* was responsive to these physical changes. Under conditions of thermal stratification, this species appeared to aggregate in the upper half of the water column (Figure 1). However, it was dispersed throughout the whole water column after the lake went into overturn (Figure 1).

Morisita's index was used to investigate quantitatively these qualitative observations. The species examined consistently showed an aggregated pattern of dispersion throughout the period of sampling (Table 1). However, temporal variations in the magnitude of Morisita's index indicated that there were considerable variations in the degree of aggregation shown by each species over the sampling period (Figure 2). Preliminary examination of these values suggested that the highest values of Morisita's index, and therefore the most pronounced aggregation, occurred during the thermally stratified period (between days 130, the 9th May, and 270, the 26th September, in Figure 2). This was particularly apparent for the two cladocerans and the two calanoid copepods.

These variations in dispersion were correlated with differences in the degree of thermal differentiation of the water column, as indicated by the water column temperature difference (WCTD). The WCTD was lowest at the start and at the end of the year, during periods of overturn, and was highest when the lake was stratified from spring to late summer (Figure 3). With the exception of *M. leuckarti*, a significant positive relationship between water column temperature difference and Morisita's index was detected (Table 2). This indicated that crustacean zooplankton populations were becoming more heterogeneous in the vertical plane with increases in the intensity of thermal stratification.

Calculation of the proportion of the population falling both above and below the maximum vertical temperature gradient on each date, showed that there was clear vertical differentiation in the abundance of each species which coincided with

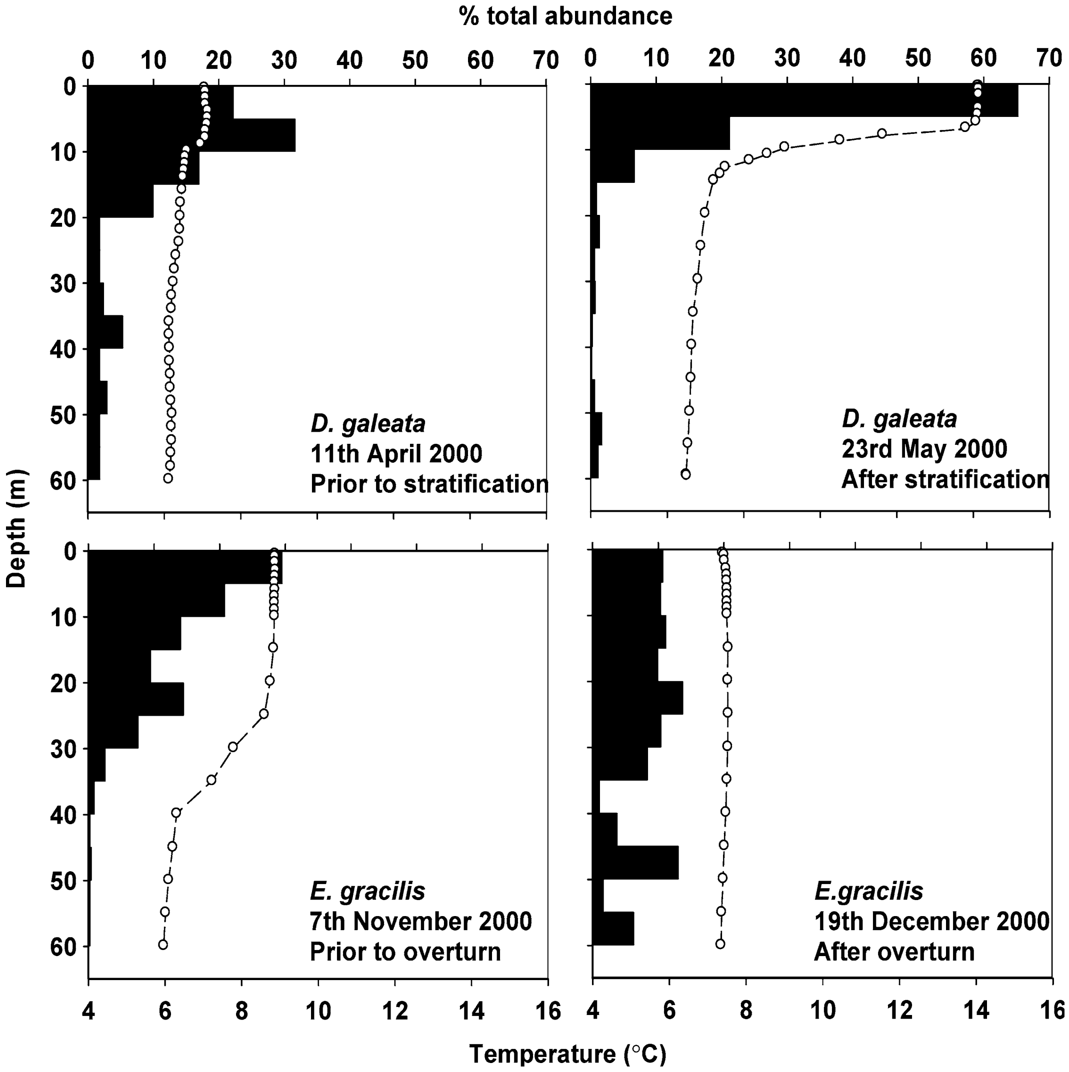

Figure 1. The vertical distribution of *D. galeata* and *E. gracilis* (bars) and vertical variations in water temperature (dotted line) during the onset and erosion of thermal stratification in spring and autumn, respectively. For each species, on each date, the abundance at a given depth is expressed as a percentage of the total abundance of that species in the water column.

Table 1. Tests for vertical aggregation in different crustacean zooplankton species using Morisita's index.

	28/3	11/4	25/4	9/5	23/5	6/6	20/6	10/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	7/11	21/11	5/12	19/12
Daphnia galeata	1.53	2.30	1.98	9.53	5.70	7.30	2.31	4.80	2.55	2.20	2.79	5.12	4.01	4.96	3.63	1.76	1.52	1.17	1.59
Bosmina obtusirostris	1.24	1.39	2.67	1.84	1.79	2.85	1.54	3.54	2.39	4.89	2.79	2.53	2.72	3.28	2.95	1.86	1.51	1.54	1.28
Eudiaptomus gracilis	1.61	1.73	3.51	4.86	4.01	3.00	3.28	2.71	4.40	3.44	2.82	6.77	4.42	3.31	2.04	2.28	1.79	1.48	1.24
Diaptomus laticeps	1.29	1.10	1.14	1.19	1.66	2.52	2.97	9.96	5.08	4.41	3.41	2.42	2.24	1.60	1.80	2.03	2.07	1.19	1.44
Cyclops s. abyssorum	2.14	1.42	2.30	4.31	2.19	1.92	2.63	3.57	2.50	2.22	2.69	1.80	2.01	2.54	1.96	2.12	1.84	1.68	1.27
Mesocyclops leuckarti	1.82	1.38	1.92	7.67	5.98	4.78	7.07	3.77	5.26	5.75	4.15	4.31	3.77	12.00	7.02				

Each column represents a different sampling date, and blank cells denote dates where a given species was absent from the community. All indices are indicative of significant departures from randomness at $p < 0.001$.

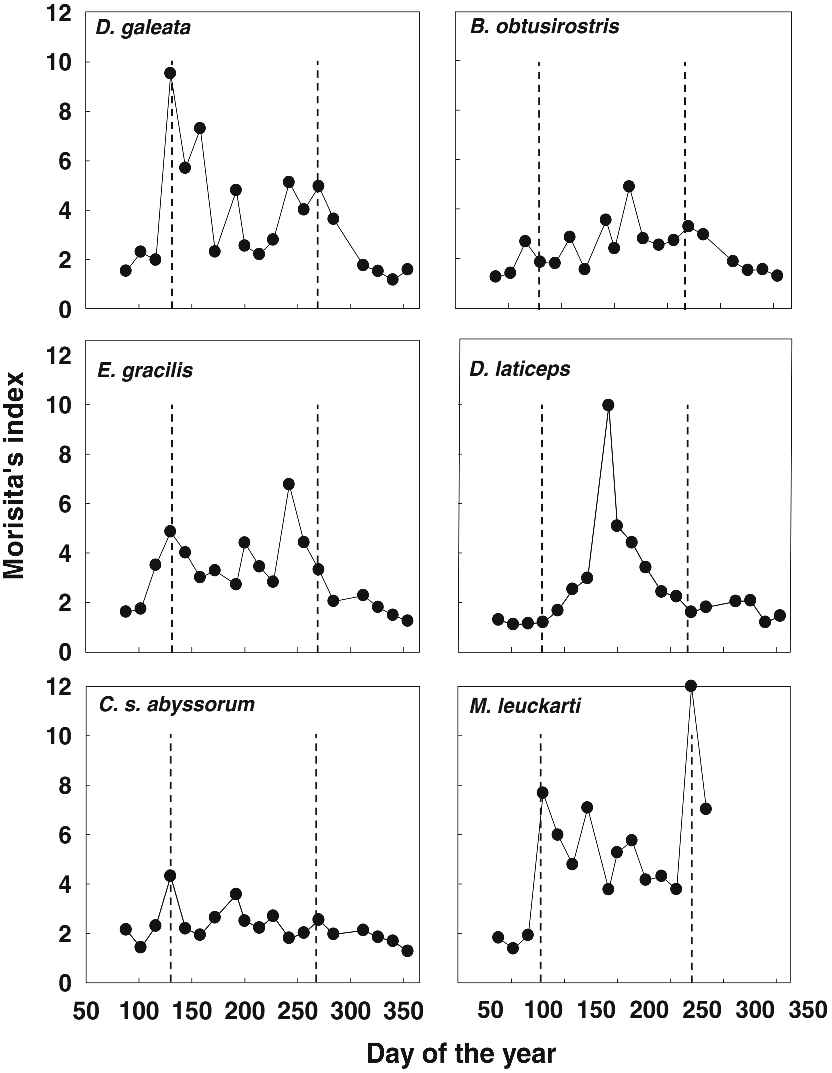

Figure 2. Temporal variations in the value of Morisita's index for each of the dominant zooplankton species. The start and end of the period of thermal stratification, defined as the period over which the maximum temperature gradient exceeded 1 °C m^{-1}, is denoted by vertical dashed lines.

the position of the thermocline. *B. obtusirostris*, *D. laticeps* and *C. s. abyssorum* were found primarily below the thermocline during the period of thermal stratification (Figure 4). In contrast, the pattern of vertical differentiation in *E. gracilis* abundance altered during the summer period. At the start and end of the period of thermal stratification, this species was most abundant above the thermocline (Figure 4). However, in the intervening period, this species was most abundant below the thermocline. A similar pattern was found for *D. galeata*, though in this case the two periods during which this species was epilimnetic in distribution were separated by a period during which this species was almost equally abundant in the epilimnion and hypolimnion. For much of the stratified period, *M. leuckarti* was most abundant in the epilimnion. With the exception of *D. galeata* and *M. leuckarti*, the difference between the proportion of the population inhabiting the region above the thermocline and the proportion inhabiting the region below the thermocline, during the stratified period, was positively correlated with the WCTD (Table 3).

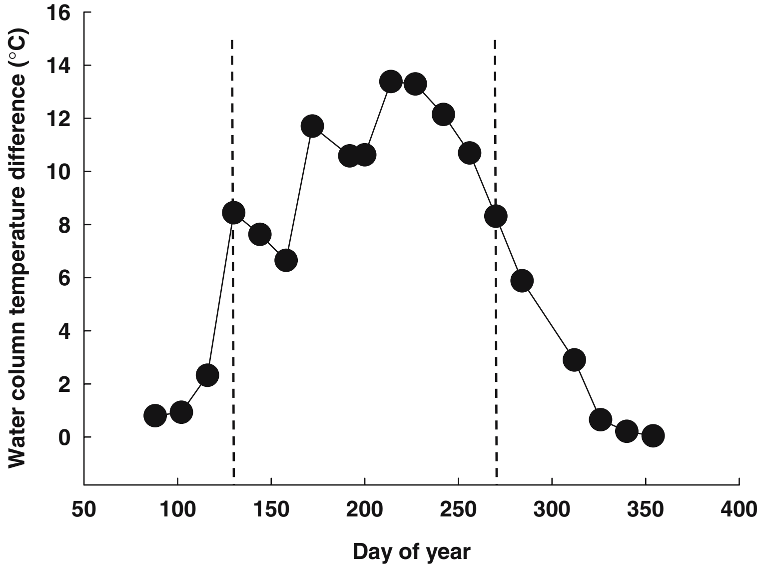

Figure 3. Temporal variation in the water column temperature difference (maximum recorded temperature minus minimum recorded temperature) at the deepest point of the north basin of Windermere. The start and end of the period of thermal stratification, defined as the period over which the maximum temperature gradient exceeded 1°C m^{-1}, is denoted by vertical dashed lines.

Discussion

The crustacean zooplankton populations of Windermere were characterised by marked vertical spatial heterogeneity, with all species showing consistently aggregated patterns of dispersion during the study period. Furthermore, there was evidence to suggest that there was a statistically detectible effect of seasonal changes in the physical structure of the water column on the degree of aggregation shown by these populations, as measured using a dispersion index approach. Most of the dominant crustacean zooplankton species became more aggregated in the vertical plane with increases in the thermal differentiation in the water column. The cyclopoid copepod *Mesocyclops leuckarti* provided the only exception to this general trend.

Table 2. Spearman's Rank correlation coefficients (r_s) for associations between Morisita's index and water column temperature difference.

Species	r_s
Daphnia galeata	0.63**
Bosmina obtusirostris	0.66**
Eudiaptomus gracilis	0.71***
Diaptomus laticeps	0.73***
Cyclops s. abyssorum	0.60**
Mesocyclops leuckarti	0.44^{ns}

ns = $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

It is recognised that dispersion statistics, such as Morisita's index, suffer the weakness of using no *explicit* spatial information (in this case depth). Significant non-randomness in dispersion, using this approach, indicates merely that an organism is markedly more abundant in some sampling units than in others. It does not indicate that the arrangement of sampling units in space is such that these variations in abundance form well-defined gradient or patch-like spatial structures, let alone that these spatial variations in abundance coincide with spatial environmental gradients. Set in the present context, the values of the dispersion indices alone do not indicate the extent to which depth-wise variations in zooplankton abundance coincide with vertical variations in water temperature.

Complementary analysis of vertical differentiation in the abundance of each zooplankton species, across the thermocline, did reveal that this statistically-detected aggregation was manifested as spatial discontinuities in zooplankton abundance. Some species were much more abundant in the hypolimnion (*Bosmina obtusirostris*, *Cyclops strenuus abyssorum* and *Diaptomus laticeps*), whilst others shifted between the epilimnion and

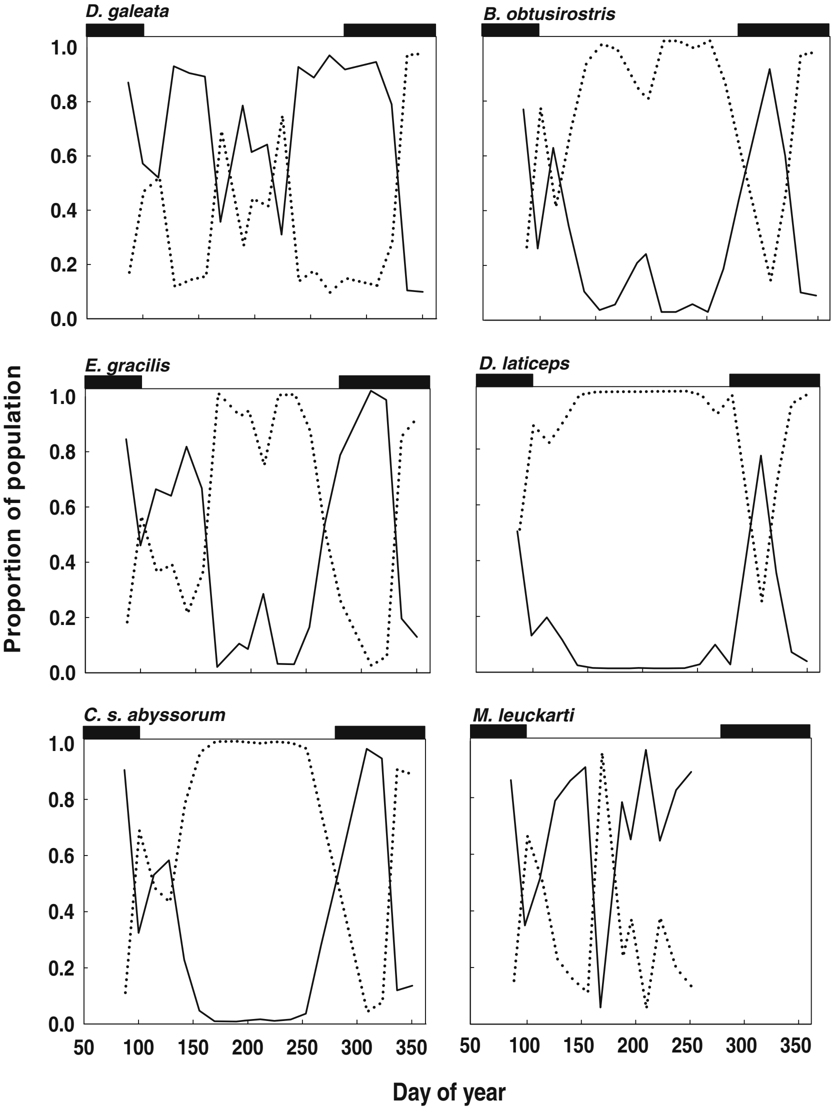

Figure 4. The proportional distribution of the dominant zooplankton species across the thermocline. Each panel shows the proportion of the population found above the thermocline (solid line) and below the thermocline (dotted line) on each date. Dark barks indicate the periods when the maximum water column temperature gradient was less than 1 °C m^{-1}.

metalimnion or hypolimnion (*Daphnia galeata*, *Eudiaptomus gracilis* and *Mesocyclops leuckarti*). Furthermore, the difference in abundance between the epilimnion and hypolimnion increased with increasing water column temperature differentiation for 4 out of 6 species. There are two possible mechanisms for this association. The first is that the increasing temperature differentiation results in increasing environmental heterogeneity, to which individual zooplankters *actively* respond, generating population-level vertical heterogeneity. The second is that reductions in the thermal differentiation of the water column are coincident with the erosion and deepening of the seasonal thermocline, during which individual zooplankters may be *passively* redistributed between the epilimnion and hypolimnion. Correlation analysis between the depth of the maximum temperature gradient and the magnitude of the difference in zooplankton abundance between the epilimnion and hypolimnion revealed no significant correlations (results not shown), therefore indicating

Table 3. Spearman's Rank correlation coefficients (r_s) for associations between the difference in the proportion of the total zooplankton population inhabiting the epilimnion and hypolimnion, and water column temperature difference.

Species	r_s
Daphnia galeata	-0.19^{ns}
Bosmina obtusirostris	0.62*
Eudiaptomus gracilis	0.64*
Diaptomus laticeps	0.70*
Cyclops s. abyssorum	0.66*
Mesocyclops leuckarti	0.30^{ns}

ns = $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

that the vertical discontinuity in zooplankton abundance became more pronounced, with increasing environmental heterogeneity, generated by strengthening water column structure.

Dispersion analyses indicated that crustacean zooplankton became more 'patchy,' as physical structuring of the water column became more pronounced. This statistically detected aggregation was apparent as vertical discontinuities in abundance between the epilimnion and hypolimnion. In a temperate lake, such as Windermere, the single biggest driver of this dynamic change in dispersion will be the transition between conditions of mixing and stratification. When the lake is thermally stratified a multitude of biologically relevant variables will become spatially structured, creating a more structured environment overall. In this way temperature structure is being used as a proxy for total environmental structure. Given that organisms aggregate where particular ecological requirements are met, this will lead to an increasing degree of organism patchiness (Begon et al. 1996).

The present results therefore provide quantitative evidence that the vertical distribution of the zooplankton is affected by thermal stratification, but cannot reveal the mechanism behind this biological response. The mechanism that links vertical heterogeneity in water temperature and zooplankton dispersion may be direct. For crustacean zooplankton rates of individual development, ingestion and assimilation as well as population birth and death rates are highly temperature dependant (Work and Gophen 1999; Hall and Burns 2002; Halsband-Lenk et al. 2002). The observed distribution patterns may, therefore, reflect direct behavioural responses of individual zooplankters to vertical gradients in water temperature, resulting in the aggregation of individuals of each species within depth ranges typified by temperatures that are optimal for growth and development (Kessler and Lampert 2004).

Once vertical swimming movements of crustacean zooplankton have been initiated, as part of diel migratory behaviours, vertical temperature gradients can be one of the primary environmental cues that modify depth selection behaviour (Ringelberg 1995). Such a mechanism may account for the observed shifts in the vertical distribution of *Eudiaptomus gracilis* and *Daphnia galeata* in the present study. Both species spent the first part of the stratified period in the epilimnion, descending to the hypolimnion and metalimnion, respectively, later in the summer. As the present sampling programme was conducted during daylight hours, this may represent the presence of inducible migratory behaviour in these species, a phenomenon observed for these taxa elsewhere (Ringelberg et al. 1991a, b).

However, it is also possible that the results reflect an indirect response of planktonic crustaceans to thermal stratification. Thermal stratification allows vertical heterogeneity in a number of ecologically influential variables (Ruttner 1953). In a stratified lake the distribution of phytoplankton will be heterogeneous in the vertical plane (Harris and Smith 1977; Reynolds 1984), introducing marked vertical gradients in the availability of food resources for herbivorous species. As different species vary in the ingestible carbon requirements needed for survival, this may introduce vertically-resolved microhabitats, differing in the availability of food resources, that allow the coexistence different species. For example, *Eudiaptomus gracilis* has a lower ingestible carbon requirement than *Daphnia* spp. (Lampert and Muck 1985), and this trait may be viewed as adaptive based on the results of the present study. The daytime depth of the calanoid was below the thermocline for much of the summer, whereas the cladoceran was metalimnetic in distribution. In the hypolimnionm below the euphotic zone, we might expect lower densities of edible phytoplankton. However, we must be cautious in attributing proximate and ultimate causes for the observed patterns of distribution, especially when vertical distribution varies over the diel cycle; at a finer temporal resolution than that of the present study.

Furthermore, individuals of each zooplankton species act as competitors and predators of individuals of other species and are therefore functionally important in the pelagic zooplankton community (Lampert and Sommer 1997). It follows that increasing vertical heterogeneity in each zooplankton species during the stratified period, generates vertical gradients in the intensity of competition and predation. It may be expected that these biological gradients will in turn influence the vertical distribution of the component species of the community (Sandercock 1967; Angeli et al. 1995). The possible mechanisms behind the relationship between water column physical structure and vertical dispersion are therefore many and complex. Whatever the mechanism behind the observed variations in dispersion, this study has provided quantitative evidence of 'zooplankton stratification' (Hofmann 1975; Miracle 1977), and clearly indicates that patterns of dispersion vary in a temporal dimension (Taylor et al. 1978).

Conclusions

This approach has shown that, in standing waters, seasonal changes in the physical structure of the water column can have statistically detectable effects on the vertical dispersion of planktonic organisms. This backs up observations based upon earlier descriptive analyses of vertically resolved zooplankton data, providing quantitative evidence for 'zooplankton stratification.'

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