Quantitative analysis of the importance of wind-induced circulation for the spatial structuring of planktonic populations.

Stephen J. Thackeray[1,3], D. Glen George[2], Roger I. Jones[1,4] and Ian J. Winfield[2]

[1] Department of Biological Sciences, Institute of Environmental and Natural Sciences, University of Lancaster, Lancaster, United Kingdom LA1 4YQ.

[2] Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP.

[3] Current address: Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP. Email: sjtr@ceh.ac.uk

[4] Current address: Department of Biological and Environmental Science, University of Jyväskylä, PL 35, 40014 Jyväskylän Yliopisto, Finland.

Corresponding author: S. J. Thackeray

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SUMMARY

1. Several studies have shown that wind-induced water movements have an important effect on the spatial distribution of crustacean zooplankton. However, few attempts have been made to quantify the effect of physical processes on these broad-scale patterns. Much of our understanding of this spatial structure has been based on the results of isolated surveys which do not capture the dynamic nature of the pelagic environment.

2. In this study, we have used a combination of high-speed sampling (at a spatial resolution of 240 m) and spatial data analysis to quantify the factors influencing the horizontal spatial structure of the *Daphnia galeata* population in Windermere.

3. The results show that lake-wide circulation patterns, as indicated by water temperature, account for 29 – 47% of the basin-scale spatial variance in *D. galeata* abundance. However, these patterns are highly dynamic and change in response to the prevailing weather. This lack of temporal persistence means that the results of single-survey sampling campaigns must be interpreted with caution.

Introduction

Spatial heterogeneity is a common feature of ecosystems and is the product of many interacting biological and physical processes. The distribution patterns of most living organisms vary as a function of the scale of investigation, as well as with the processes that govern spatial pattern (Wiens, 1989). Over large spatial scales, physical processes are thought to have the dominant influence on the spatial distribution of organisms. At smaller scales, however, biological processes (predation, competition, reproductive behaviour) act to decouple organisms from the direct effect of many physical processes (Legendre & Demers, 1984; Wiens, 1989).

This scale-dependent hierarchy of causal factors is well recognised within the context of lake plankton ecology (George, 1981b; Malone & McQueen, 1983; Pinel-Alloul, 1995), and has been termed the “multiple driving force hypothesis” (Pinel-Alloul, 1995). At small spatial scales, planktonic crustacea exhibit swarming behaviour, resulting in the formation of patches from a few metres to tens of metres in diameter (Colebrook, 1960b; Lacroix & Lescher-Moutoue, 1995). Swarming behaviour is initiated in the presence of predators (Jakobsen & Johnsen, 1987) and can reduce the feeding efficiency of visual predators (Milinski, 1977) or reduce predator-prey encounter rates (Pinel-Alloul *et al*., 1988). Small scale aggregations of crustacean zooplankton may also facilitate mate finding (Folt & Burns, 1999).

The multiple driving force hypothesis states that physical processes, such as wind-induced circulation, have the dominant influence on basin-scale distribution patterns. Several studies have described the effect of physical processes on basin-scale plankton distribution (George & Edwards, 1976; Jones *et al.*, 1995; Kalikhman, Walline & Gophen, 1992) and related these patterns to changes in the weather. More specifically, it has been suggested that the combined action of wind-induced water movements and organism behaviour can result in large-scale spatial heterogeneity. This occurs because, when a stratified lake is subjected to direct wind forcing, surface epilimnetic water is dragged downwind, whilst a deeper return current, flowing upwind, is established lower in the epilimnion (George, 1981a; Smith, 1992). The result is that planktonic organisms with a tendency to aggregate in the upper epilimnion are moved downwind, accumulating in areas of downwelling, whereas organisms aggregating deeper in the epilimnion are accumulated in areas of upwelling. Vertical and horizontal spatial heterogeneity are thus coupled under this "conveyor belt" model of redistribution. Evidence for this mechanism of accumulation has been presented in studies of a number of systems (George & Edwards, 1976; George & Winfield, 2000; Jones *et al.*, 1995; Lacroix & Lescher-Moutoue, 1995; Ragotzkie & Bryson, 1953). Therefore, although the multiple driving force hypothesis states that behavioural mechanisms cannot directly account for basin-scale patterns in distribution, the ability of zooplankton to influence their vertical distribution permits indirect behavioural modification of large-scale horizontal pattern.

There have, however, been few attempts to quantify the importance of these physical effects by determining the proportion of the spatial variance in plankton abundance that is explained by broad-scale physical structuring of the pelagic environment. Recent developments in the analysis of spatially referenced ecological data make this possible (Legendre *et al*., 2002), provided a suitable tracer of lake physical structure is available. Many previous studies actually reported the results of surveys that took many hours or days to complete (Kalikhman, 1999; Pinel-Alloul *et al*., 1999), yet spatial pattern in lacustrine environments shows a high degree of temporal variability. Dynamic changes in the physical structure of the pelagic environment cause distribution patterns of planktonic organisms to vary over time (George & Edwards, 1976; Jones *et al.*, 1995; Ragotzkie & Bryson, 1953). As a result, there is a real possibility that sampling design may generate artefactual spatial patterns when surveys take a long time to complete (Avois *et al*., 2000). Also, much of our understanding of the spatial ecology of plankton communities has been based upon studies that report the results from only one sampling date (Lacroix & Lescher-Moutoue, 1995; Pinel-Alloul, 1999; Malone & McQueen, 1983) and, as a result, they do not adequately reflect the dynamic nature of spatial pattern in pelagic communities. Our understanding of the spatial structuring of aquatic ecosystems would be furthered by studies which adopt a quantitative approach to examining physical determination of spatial pattern over a series of survey dates.

In the present study, the horizontal distribution of a single zooplanktonic species was examined over a series of sampling dates during 2000 and 2001. Data from three of these dates are presented, chosen to reflect the range of variability in zooplankton spatial pattern and in its relationship with the physical environment. Data were collected using high-speed sampling to minimise the confounding effects of short-term temporal variation in spatial pattern, and a quantitative approach was adopted for the analysis of spatial structure. Though it is recognised that zooplankton heterogeneity is in reality affected by a multitude of driving variables, our purpose was to focus upon one of these variables. Given the emphasis placed upon the primacy of physical processes in the generation of large-scale spatial patterns, the aim of this study was to quantify the effect of these in-lake physical processes. Firstly, it was hypothesised that large-scale spatial variability in zooplankton abundance will be shared with that in the physical environment. Secondly, it was hypothesised that the nature of spatial pattern and of the association between the physical environment and zooplankton heterogeneity will vary over time.

Methods

Sampling site

The present study was conducted in Windermere, Cumbria, United Kingdom (54°20’N, 2°57’W; Fig. 1). In terms of length (17 km) and volume (314.5 x 10^6 m^3), it is the largest of the English Lake District lakes (Ramsbottom, 1976). Windermere comprises two distinct basins separated by a region of shallows and islands. All fieldwork was carried out in the north basin (surface area, 8.05 km^2; volume, 201.8 x 10^6 m^3; maximum depth, 64 m).

Insert Fig. 1

The physics, chemistry and biology of Windermere have been monitored for over sixty years. As a result, the seasonal dynamics of the phytoplankton, zooplankton and fish communities are well understood (Frost, 1965; Le Cren, 1987; Reynolds & Irish, 2000; Smyly, 1968; Wailes, 1939). Also, the bathymetry and hydrodynamics of the lake are rather simple and well described (Colebrook, 1960a; George, 1981a; Ramsbottom, 1976). Consequently this is an excellent system within which to study the effects of physical processes on plankton distributions.

In the present study, circulation patterns were not measured directly. Rather, subsurface measurements of water temperature were used to make inferences about the physical structure of the pelagic zone. If horizontal variations in water temperature are recorded over a short period of time, they may be treated as a relatively conservative indicator of wind-induced water movements (Mortimer, 1952). Synoptic drogue/drift bottle releases and temperature measurements have found this to be the case in Windermere (George, 1981a). Under conditions of direct wind forcing, warmer surface water accumulates downwind, whilst cooler subsurface water upwells upwind. The result is an increase in subsurface water temperature from the windward to the leeward end of a lake.

The crustacean zooplankton community of Windermere is dominated by only six species: 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). The present study focuses on the spatial dynamics of *D. galeata*, which was the only abundant epilimnetic zooplankter at the time of sampling.

Field methods

Horizontal variations in zooplankton density and in water temperature were recorded, using a modification of the flow-through sampling system described by George (1976) to collect a sequence of spatially distinct samples, while traversing a series of transects spanning the north basin. A length of reinforced hose (internal diameter approximately 25 mm) was towed behind a research vessel. On the deck of the research vessel the hose was attached to a self priming pump, which pulled water up from below the lake surface and passed it to a flow cell housing a thermistor. This recorded the temperature of the lake water (± 0.02 °C) and communicated this information to a microcomputer. A pressure transducer was also attached to the hosepipe, close to the inlet, in order to record accurately (± <0.01 m) the depth of sampling. By attaching the end of the hose to a 2.5 kg Scripps depressor, the sampling depth was stabilised at approximately 3 m (± 0.2 m). The microcomputer automatically recorded the output from each sensor at 1 min intervals during sampling.

After leaving the flow cell, the lake water was passed through one of a pair of mesh concentrating funnels (mesh size = 120 μm), before being discharged overboard. This allowed collection of the crustacean zooplankton from the flow of water. The outlet of the sampling device was attached to a two-way tap so that, at regular time intervals, the continuous flow of lake water could be redirected between the pair of mesh concentrating funnels. While one funnel was in use, the sample collected in the other was rinsed into a vial and preserved in a 4% solution of formaldehyde. By redirecting the flow in this way, a series of spatially distinct zooplankton samples was collected. The flow of water was redirected every 3 min, such that each horizontal sample was integrated over approximately 240 m. The spatial resolution of the survey was therefore appropriate for the analysis of large-scale physical determination, though not for the identification of behavioural/biological drivers of heterogeneity. For reasons of consistency, the output from the sensors in the flow-through system was averaged over each 3 min sampling interval. Species were subsequently identified under a binocular microscope according to the keys of Scourfield & Harding (1966) and Harding & Smith (1974), and samples were counted in their entirety.

Survey design constituted a series of 10 transects, spanning the north basin (Fig. 1). The transects were arranged in a zig-zag fashion in order to maximise the spatial coverage of the survey for the distance travelled. During sampling, the research vessel cruised at a speed of approximately 80 m min^{-1}, allowing each horizontal survey to be completed in approximately 2 h. The geographic position of the boat was recorded at 5 s intervals during each sampling run using a differential GPS system (TSC1 Asset Surveyor and Pro XR Receiver, Trimble Navigation). The location of each temperature measurement and zooplankton sample was determined by matching the time of collection to the relevant time on the GPS trace.

The vertical distribution of crustacean zooplankton was investigated at a station above the deepest point of the north basin (Fig. 1). During 2000, the vertical distribution of *D. galeata* was sampled using a messenger activated closing net (mesh size, 120 μm; mouth diameter, 250 mm). The upper 60 m of the water column was divided into a series of 12 5 m-deep strata and, on each sampling occasion, the closing net was drawn once through each of these strata, filtering approximately 245 L of water. During 2001, the flow-through sampling system was used to sample the fine scale vertical distribution of zooplankton within the epilimnion. Zooplankton samples were collected at 1 m intervals throughout the upper 15 m of the water column.

Meteorological data were obtained from an Automatic Water Quality Monitoring Station (AWQMS) on nearby Esthwaite Water and an automated weather station at the Windermere site of the Centre for Ecology and Hydrology (CEH), positioned at the southern extreme of the north basin. Wind speed and direction were logged at hourly intervals from each of these locations. In order to summarise and illustrate recent wind history, easterly and northerly components of wind velocity were calculated from the hourly data for 1 d prior to each sampling date. Although wind data were only available from the Esthwaite Water AWQMS during 2001, comparisons between this source and the CEH Windermere weather station have shown that wind direction data from these two sites are comparable (CEH Windermere, unpublished data).

Statistical analysis

Methods of spatial data analysis were used to explore the horizontal data. All analyses were carried out in the R environment (Ihaka & Gentleman, 1996) and using programs created by Legendre & Vaudor (1991).

Prior to analysis, data were tested for normality using the Shapiro-Wilks test and, where necessary, normalised by Box-Cox transformation (Sokal & Rohlf, 1995). The spatial structure of the measured variables was investigated by constructing correlograms, using Geary's c autocorrelation statistic (Geary, 1954). The statistic takes values <1 when sites at a given separation distance are positively autocorrelated and values of >1 when sites are negatively autocorrelated. When Geary's c equals one, sites are independent with respect to the variable being analysed. Distance classes were delimited such that they contained equal numbers of paired observations (Pinel-Alloul *et al*., 1999). This ensured that each autocorrelation statistic could be viewed with equal confidence. As each correlogram was based on the testing of a number of autocorrelation statistics, the global significance of each correlogram was assessed using the Bonferroni procedure to adjust the significance level for the number of simultaneous tests being performed (Pinel-Alloul *et al*., 1999). Since 10 autocorrelation statistics were calculated for each correlogram, each value of Geary's c was assessed at both $p<0.05$ and the adjusted significance level of $p<0.005$ (= 0.05/10). In Figs. 2 – 4, individual values of Geary's c are categorised as statistically significant at $p<0.05$, $p<0.005$ or non-significant ($p>0.05$).

The associations between water temperature and zooplankton abundance were investigated by correlation analysis, using a method where the *t*-test of the correlation coefficient had been modified to take account of spatial autocorrelation (Dutilleul, 1993). Classical correlation analyses are often inappropriate in the analysis of associations between spatially structured variables, which violate the assumption of independence required for hypothesis testing. The result of this interdependence is that each observation does not contribute a whole degree of freedom, and the correct reference distribution of the test statistic is not chosen (Legendre & Fortin, 1989). In Dutilleul's method, the degrees of freedom of the *t*-test statistic are calculated on the basis of an "effective sample size" which, for positively autocorrelated processes, is typically less than the number of sampling locations. The method has also been proven to counteract the inflated type I error rate resulting from the presence of broad-scale spatial structure (Legendre *et al*., 2002).

During analyses of the spatial relationships between ecological variables, correlations may be generated by two mechanisms. Firstly, a significant correlation may reflect a genuine association between the measured variables. A second mechanism is that both variables may have been independently structured by a third spatially structured (unmeasured) variable. The method proposed by Legendre *et al* (2002) was used to establish which of these mechanisms explained the correlations between water temperature and zooplankton density and to quantify the effect of physical determination on the distribution of zooplankton, by calculating the proportion of spatial variance in *D. galeata* density shared with that in water temperature. This analysis comprised three steps. Firstly, the explanatory variable (water temperature) was regressed onto its coordinates in order to model its broad-scale spatial structure. All terms for a cubic trend surface were included in the regression, thus:

$$z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \qquad (1)$$

Where z is the predicted value of variable z, b_1 to b_9 are regression coefficients, x is the easting and y is the northing (Borcard, Legendre & Drapeau, 1992). Prior to analysis, spatial coordinates were centred to a mean of zero. All terms were initially included in a stepwise regression, but only those that explained a significant proportion of the variability in the explanatory variable were retained when producing the final trend surface model. It is important to include initially all of the terms for a cubic trend surface, so that relatively complex spatial patterns can be described as a function of the coordinates. The absence of the higher order terms would restrict the spatial model to the description of simple linear trends, rendering it inadequate for the analysis of more complex, patch-like structures. Secondly, the response variable (zooplankton density) was regressed onto the fitted values from the first regression, thus modelling shared broad-scale structure. The coefficient of determination of this regression provides an unbiased estimate of the shared broad-scale spatial variation between the two variables. Finally, the partial correlation between the residuals from the two regression analyses was assessed in order to determine the association between the two variables; independent of any shared deterministic structure. During this analysis the partial *t*-statistic and corrected degrees of freedom were calculated by modifying those calculated in Dutilleul’s correlation method, to take account of the number of parameters in the broad-scale spatial model (Legendre *et al.*, 2002).

Results

20 June 2000

Sampling on 20 June 2000 followed a period of south-westerly winds (Fig. 2a). Water temperature was highest in the north and east of the basin, with a range of approximately 3 ºC (Fig. 2c). The spatial structure could be described by a basin-scale gradient: positive autocorrelation was found at distances of up to 1.3 km and negative autocorrelation at distances above 3 km (Fig. 2f). This indicated that the physical structure of the pelagic zone was affected by the agency of an underlying large-scale, non-random process i.e. external forcing by the wind. Horizontal variation in water temperature clearly reflected the downwind movement of surface waters.

Insert Fig. 2

On this date *D. galeata* were aggregated in the upper epilimnion (Fig. 2b). Horizontally, the highest densities of this species were found in the northern and eastern parts of the basin, coinciding with regions of high water temperature (Fig. 2d). The population density of *D. galeata* was significantly structured at a broad spatial scale (Fig. 2g). In the correlogram, the only two significant coefficients (at the Bonferroni corrected error rate of $p<0.005$) indicated positive autocorrelation at distances of ~ 0.5 km and negative autocorrelation at distances above ~3.8 km. A significant positive correlation was observed between *D. galeata* density and water temperature ($r = 0.74$, $t = 2.85$, df = 6.91, $p<0.05$).

Stepwise regression of water temperature on the matrix of spatial variables produced a trend surface of the form:

$$z_i = b_1 X i + b_2 Y_i + b_3 X^2_i + b_4 X^2 Y_i + b_5 Y^3_i \qquad (2)$$

The trend surface provided a good fit of the broad-scale variation in water temperature ($F_{5,30} = 66.90$, $p<0.001$, $r^2 = 0.90$). Regression of *D. galeata* density on the spatial model for water temperature indicated that almost half of the spatial variation in *D. galeata* density was shared with spatial variations in water temperature ($F_{1,34} = 32.20$, $p<0.001$, $r^2 = 0.47$).

After removing the spatial structure “passed on” from the physical environment on 20 June 2000, no further spatial structuring in *D. galeata* density was evident (Fig. 2e & h): the more localised variations in residual *D. galeata* density were indistinguishable from randomness. *Daphnia galeata* abundance and water temperature were not significantly correlated in the absence of their shared broad-scale structure ($r = 0.32$, $t = 1.35$, df = 28.5, $p = 0.06$).

1 August 2000

On the 1 August 2000, following a period of south westerly winds (Fig. 3a), a south-north gradient of increasing water temperature was recorded (Fig. 3c). This reflected downwind convergence of surface waters, with some current rotation. A significant basin-scale gradient in water temperature was confirmed by correlogram analysis (Fig. 3f). *Daphnia galeata* was most abundant in the upper epilimnion (Fig. 3b) and, horizontally, the density of this species was higher in the northern, warmer, part of the basin (Fig. 3d). Correlogram analysis suggested significant basin-scale spatial heterogeneity in *D. galeata* density (Fig. 3g).

Insert Fig. 3

The association between *D. galeata* density and water temperature was characterised by a positive correlation coefficient, though this coefficient was not statistically significant ($r = 0.59$, $t = 1.12$, df = 2.7, $p = 0.31$). However, simulation studies have shown that the presence of broad-scale structure in environmental and response variables often reduces the power of Dutilleul’s modified *t*-test procedure for evaluating the significance of correlation coefficients (Legendre *et al*., 2002).

Spatial variability in water temperature was effectively modelled by a linear combination of selected spatial variables ($F_{6,30} = 175.20$, $p<0.001$, $r^2 = 0.97$):

$$z_i = b_1X_i + b_2Y_i + b_3X^2_i + b_4X^2Y_i + b_5XY^2_i + b_6Y^3_i \quad (3)$$

Regression of *D. galeata* density on this broad-scale spatial model for temperature confirmed that almost a third of the variation in *Daphnia* abundance was shared with that in water temperature ($F_{1,35} = 15.92$, $p<0.001$, $r^2 = 0.29$).

Spatial structuring of *D. galeata* density was still evident after the removal of broad-scale variation shared with that in the physical environment. Residual variation in *D. galeata* density was characterised by a patch-like structure (Fig. 3e & h). A transition from positive to negative autocorrelation occurred over distances of approximately 0.75 km. Positive autocorrelation was again evident, at distances of just over 1 km, representing the distance between patches. At greater distances, sites were independent in terms of residual *D. galeata* density. A significant correlation between *D. galeata* density and water temperature was not detected after the removal of broad-scale physical structure ($r = 0.28$, $t = 1.10$, df = 18.21, $p = 0.17$).

20 June 2001

Following a period of southerly, south-easterly and south-westerly winds (Fig. 4a), an increase in water temperature was observed between the south and north of the basin, reflecting the downwind movement of warm surface waters (Fig. 4c). Spatial variations in *D. galeata* density followed the same general trend as water temperature, being highest in the northern (downwind) part of the basin (Fig. 4d). This situation was precisely what would have been expected if *D. galeata* aggregated in the upper epilimnion. Fine resolution vertical data, obtained by using the flow-through sampling device to collect a series of zooplankton samples at 1 m depth intervals over the upper 15 m of the water column, showed that this was the case (Fig. 4b).

Insert Fig. 4

Correlogram analysis showed that water temperature was spatially structured at the basin-scale and was typical of a large-scale gradient (Fig. 4f). Correlogram analysis failed to detect significant basin-scale spatial structure in the distribution of *D. galeata* (Fig. 4g). Positive autocorrelation was detected among neighbouring sites (within a radius of approximately ~0.5 km). Sites at all other separation distances appeared to be independent. This was indicative of a patch-like spatial structure in *D. galeata* abundance, with 0.5 km being the approximate patch diameter.

A positive association between *D. galeata* density and water temperature was indicated, but was not statistically significant ($r = 0.68$, $t = 1.48$, df = 2.6, $p = 0.25$). The following trend surface successfully described the broad-scale variation in water temperature across the north basin, ($F_{5,29} = 68.15$, $p<0.001$, $r^2 = 0.91$):

$$z_i = b_1 X_i + b_2 Y_i + b_3 XY_i + b_4 XY^2_i + b_5 Y^2_i \qquad (4)$$

Regression of *D. galeata* density on this broad-scale spatial model for water temperature indicated that almost half of the variation in *Daphnia* abundance was shared with temperature ($F_{1,33} = 31.57$, $p<0.001$, $r^2 = 0.47$). After partialling out this shared broad-scale spatial structure, no significant correlation was found between *D. galeata* density and water temperature ($r = 0.04$, $t = 0.44$, df = 20.5, $p = 0.84$). However, there was still significant spatially structured variation in *D. galeata* density at a sub-basin scale (Fig. 4e & h). At distances of approximately 0.5 km, sites were positively autocorrelated. Sites separated by ~ 1.75 km were negatively autocorrelated. At larger separation distances, sites were independent. This residual variation in *D. galeata* density was therefore characterised by a patch-like spatial structure.

Discussion

The repeated occurrence of horizontal temperature variations on all sampling dates confirmed that a large-scale, non-random process was responsible for the generation of physical structure in the pelagic zone of the north basin of Windermere. Horizontal variation in water temperature could be understood with reference to recent wind history. Water temperature increased from the windward to the leeward end of the lake. The results of the present study, therefore, confirm that direct wind forcing is frequently a dominant influence on circulation in the north basin of Windermere. During thermal stratification and under conditions of direct wind forcing, winds drag warm surface waters toward the leeward end of the lake, resulting in horizontal current convergence and downwelling. An upwind return current is generated in the lower part of the epilimnion, such that cooler waters reach the lake surface upwind. In Windermere, these currents are deflected by the Coriolis force, resulting in a helical water flow throughout the epilimnion under conditions of direct wind stress (George, 1981a).

Zooplankton patchiness is a product of many different abiotic and biotic factors, acting at different scales. The result is a nested pattern where abiotic factors have the dominant effect on spatial structure at large spatial scales and biotic factors assume dominance at small spatial scales (George, 1981b; Pinel-Alloul, 1995). According to the classification of Malone & McQueen (1983), the spatial resolution of the horizontal surveys (240 m between-site separation distance) defines the present study as an investigation of large and fine scale pattern (10 m - > 1 km). In general there was support for the hypothesis that, at these scales, water movements affected the horizontal distribution of crustacean zooplankton in Windermere.

On the three sampling dates, the coefficients of correlations between water temperature and *D. galeata* density were rather high, ranging between 0.59 and 0.74. This suggested a positive association between water temperature and *D. galeata* density. However, only one of these coefficients was statistically significant. It is proposed that the presence of broad-scale structure in the environmental and response variables reduced the power of Dutilleul's modified *t*-test. Despite the magnitude of these correlation coefficients, the method proposed by Legendre *et al*. (2002) showed that the two variables were not correlated after the removal of their shared broad-scale structure. The variance that *D. galeata* abundance shared with water temperature was considerable: between 29% and 47%. This suggests that both water temperature and *D. galeata* density were subject to the same broad-scale structuring process but were not themselves causally linked. Rather, each was independently structured by the same underlying large-scale process (Legendre & Fortin, 1989). This is consistent with the idea that water temperature is a reflection of lake circulation and that *D. galeata* were passively redistributed by these same water movements.

On one sampling date (20 June 2000), physical structuring accounted for all of the spatially structured variation in *D. galeata* density. Although spatial variation in abundance remained after partialling out the effect of basin-scale physical structure, it proved indistinguishable from randomness. This was not the case for the other sampling dates. The remaining spatially structured variation in *D. galeata* density on 1 August 2000 and 20 June 2001 could not be correlated with spatially localised variations in the physical environment. This suggested that, on these sampling dates, another process was responsible for the generation of spatial heterogeneity in the *D. galeata* population of Windermere.

Spatial heterogeneity generated directly by behavioural mechanisms is only likely to become apparent at very fine (sub-metre) spatial scales (Folt & Burns, 1999). In the pelagic zone, biological drivers of horizontal patchiness are necessarily limited to small spatial scales by the lack of an optical cue for the orientation of horizontal swimming (Ringelberg, 1969; Siebeck, 1969). In inshore regions, the effect of the elevated horizon on the underwater angular light distribution provides a means of orientation for horizontal swimming. However, in the pelagic zone this effect is diminished and *Daphnia* display a vertical body orientation and, therefore, a primarily vertical swimming mode. As a result, a relatively weak tendency for horizontal swimming would be readily overwhelmed by physical processes at large spatial scales (George, 1981b; Pinel-Alloul, 1995). The large-scale horizontal patterns apparent in *Daphnia* abundance in Windermere are indirectly influenced by the ability of planktonic crustaceans to influence their own vertical distribution, as a result of the coupling of horizontal and vertical spatial pattern (George & Edwards, 1976). However, after partialling out the large-scale component of variation, it is unlikely that the remaining spatially-structured variation represented the aggregation of zooplankton around patches of edible phytoplankton or the avoidance of predators. Given the spatial resolution of the horizontal surveys, it would be inappropriate to seek to explain the remaining spatial variance in these large-scale surveys in terms of such biological processes (Schneider, 1994; Wiens, 1989).

The remaining spatially structured variation might be explained by temporal variations in the wind-direction, leading to current divergence and the fragmentation of previously formed zooplankton patches (Ragotzkie & Bryson, 1953). These patch-like variations in zooplankton abundance might also reflect the effect of continued accumulation of the animals downwind, under steady wind conditions, or be maintained by circulation cells (gyres) established under conditions of direct wind forcing (Falconer, George & Hall, 1991; Podsetchine & Schernewski, 1999). On any one sampling day, an assessment of the relationship between zooplankton distribution and physical structure is made using data that are an instantaneous “snapshot” of a temporally dynamic system.

Previous studies have emphasised interspecific variation in the basin-scale spatial structuring of zooplankton populations (Lacroix & Lescher-Moutoue, 1995; Malone & McQueen, 1983; Pinel-Alloul *et al.*, 1999). This study also observed considerable intraspecific variation in the spatial patterns of a single species: both small-scale (20 June 2001) and large-scale (20 June 2000, 1 August 2000) patterns were observed. It has also been stated that the physical environment may be characterised by large-scale spatial organisation, in contrast to a typically smaller scale, patch-like structure for biological variables (Pinel-Alloul *et al*., 1999). In the present study the repeated analysis of spatial structure for *D. galeata* and water temperature have revealed that this distinction between the physical and biological environment, in terms of spatial structure, is not always clear. The results of repeated surveys in the Gulf of St Lawrence have shown a similar lack of temporal persistence in the spatial structuring of zooplankton biomass (De Lafontaine, 1994). Clearly, it is not possible to make generalisations about the spatial structuring of individual zooplankton species based on the results of a single survey.

A quantitative analysis of the data has shown that, in isolation, wind-induced water movements can explain almost half of the spatial variation in *D. galeata* abundance in Windermere. Hypothesis (i), that large-scale spatial variability in zooplankton abundance will be shared with that in the physical environment, is thus supported. The observed temporal variation in the spatial organisation of the *D. galeata* population (i.e. the presence of large-scale gradient-like patterns and of smaller-scale patch-like structures) and in the proportion of variation explained by physical structure also supports hypothesis (ii): the nature of spatial pattern and of the association between the physical environment and zooplankton heterogeneity will vary over time. In the light of this temporal variability, conclusions that are drawn from single surveys or from surveys that took many hours or days to complete must be viewed with caution.

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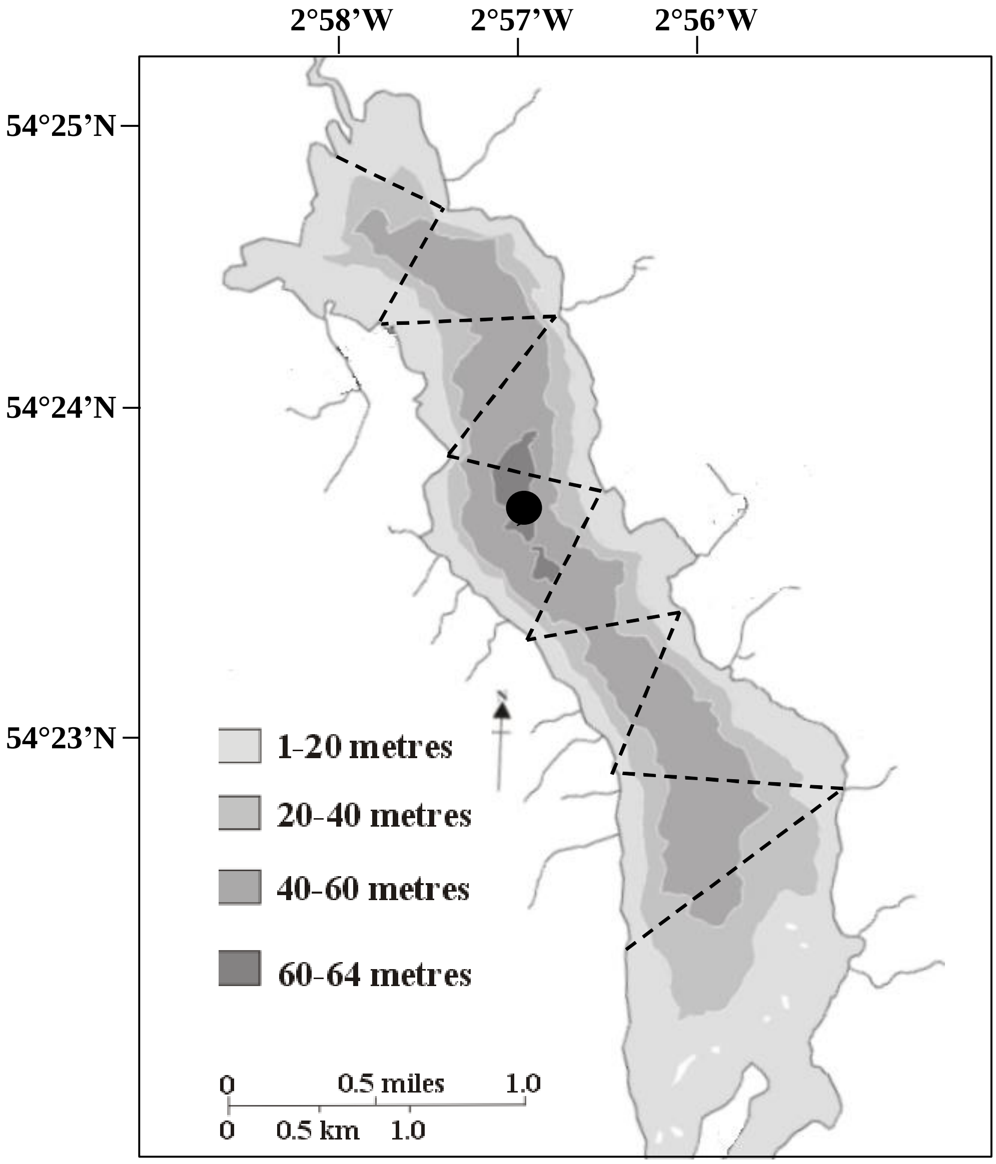
Figure legends

Fig. 1. Bathymetric map of the north basin of Windermere, showing the position of the sampling transects (dashed lines). The deepest point of the basin is also marked (closed circle).

Fig.2. Horizontal pattern and spatial structure in water temperature (c, f), *D. galeata* density (d, g), and residual *D. galeata* variation (e, h) on 20 June 2000. Spatial structure is depicted by correlograms of Geary's *c* for different distance classes. The wind history, for 24 hr prior to sampling, is depicted as a progressive vector diagram (a), and the vertical distribution of *D. galeata* relative to the thermocline is also indicated (b).

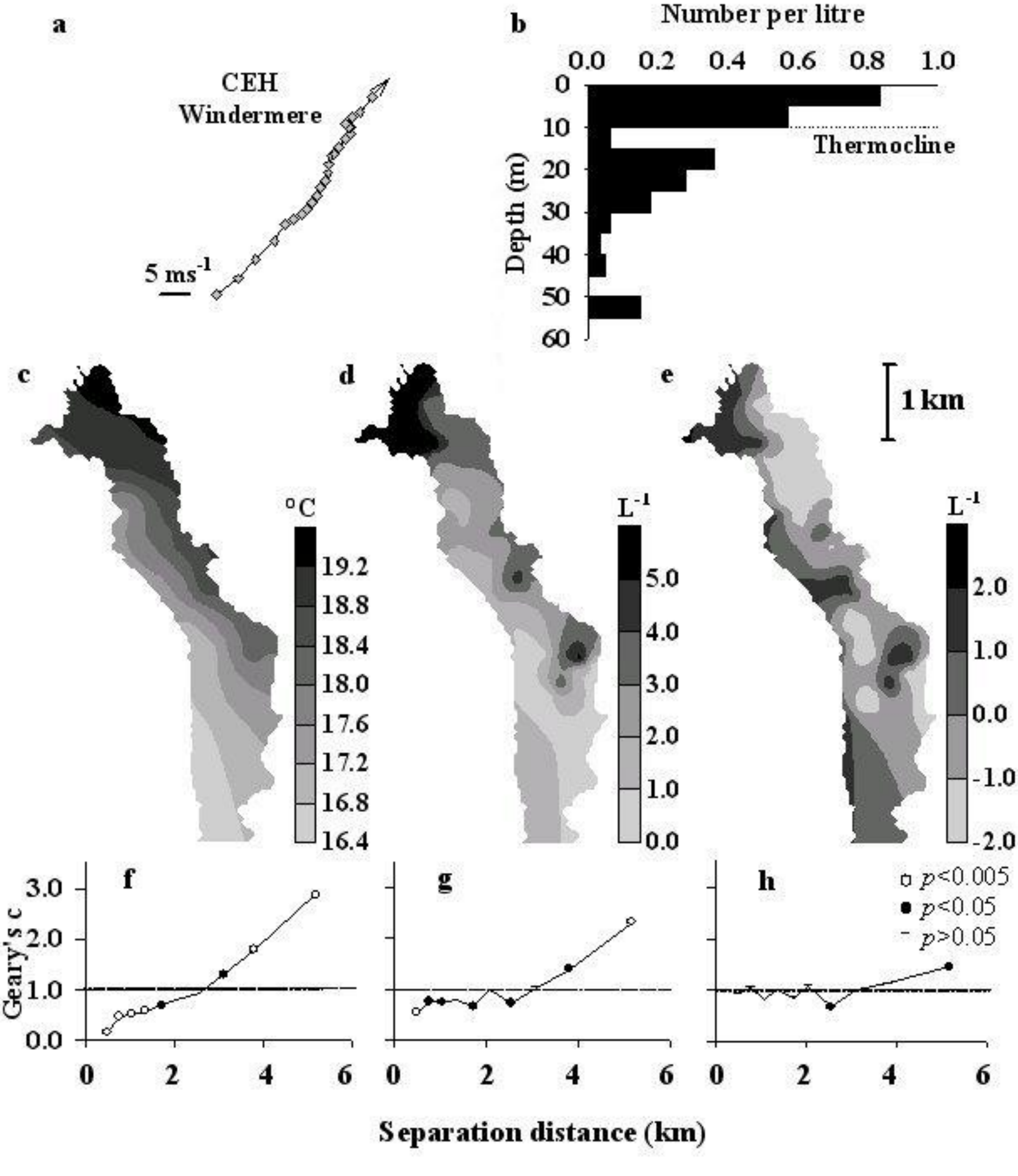
Fig. 3. Horizontal pattern and spatial structure in water temperature (c, f), *D. galeata* density (d, g), and residual *D. galeata* variation (e, h) on 1 August 2000. Spatial structure is depicted by correlograms of Geary's *c* for different distance classes. The wind history, for 24 hr prior to sampling, is depicted as a progressive vector diagram (a), and the vertical distribution of *D. galeata* relative to the thermocline is also indicated (b).

Fig. 4. Horizontal pattern and spatial structure in water temperature (c, f), *D. galeata* density (d, g), and residual *D. galeata* variation (e, h) on 20 June 2001. Spatial structure is depicted by correlograms of Geary's *c* for different distance classes. The wind history, for 24 hr prior to sampling, is depicted as a progressive vector diagram (a), and the vertical distribution of *D. galeata* relative to the thermocline is also indicated (b).



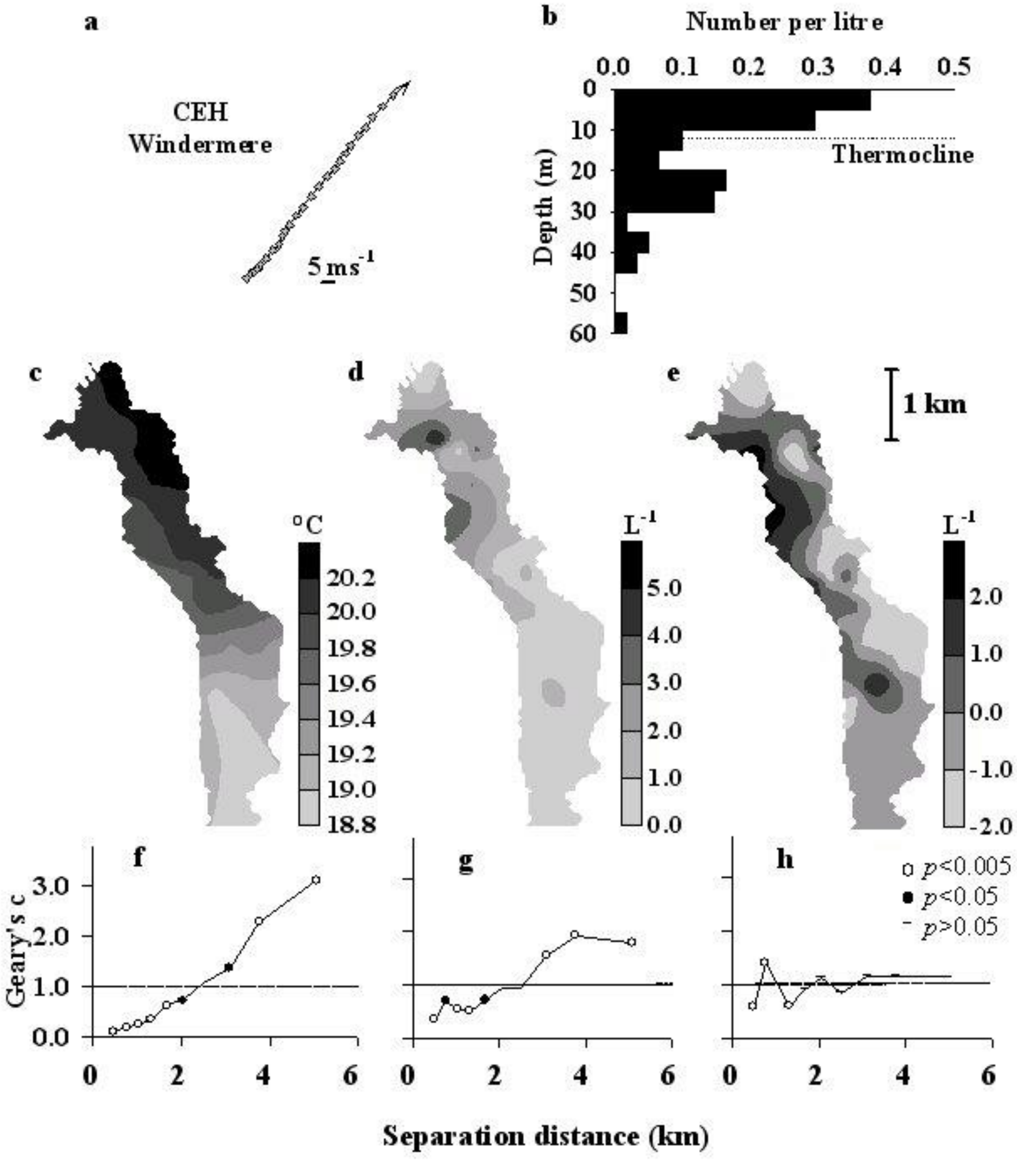
S. J. Thackeray Fig. 1

20th June 2000



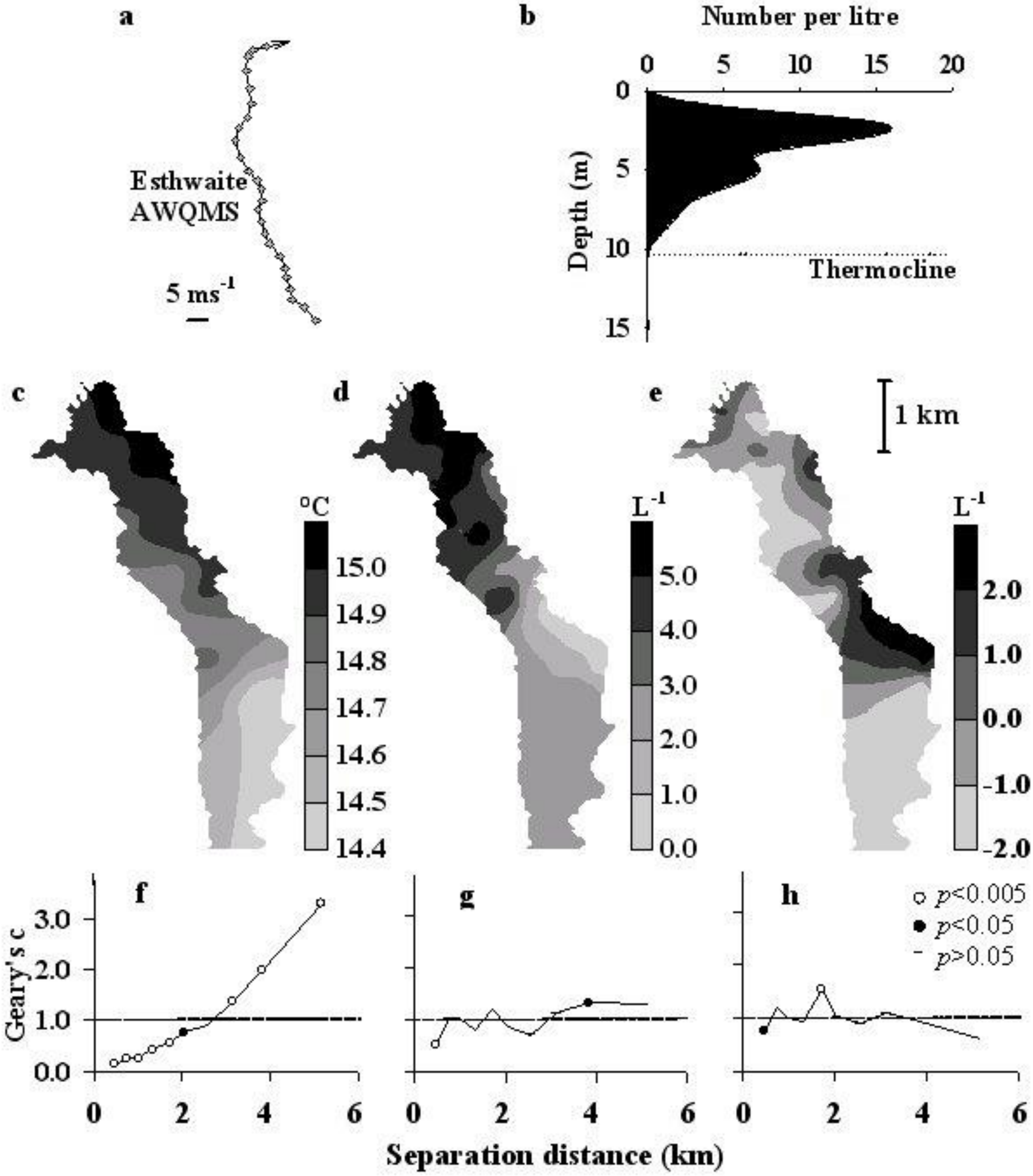
S. J. Thackeray Fig. 2

1st August 2000



S. J. Thackeray Fig. 3

20th June 2001



S. J. Thackeray Fig. 4