How internal waves influence the vertical distribution of zooplankton

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SUMMARY

1. We present data with a high spatio-temporal resolution from a 72-h field survey in Bautzen Reservoir (Saxony, Germany). The aims of this survey were to observe hydrophysical processes during a period of unstable stratification in spring and investigate the effect of wind-induced internal waves on the vertical distribution of zooplankton.
2. Wind velocities up to 10 m s⁻¹ caused a strong downwelling event of warm water at the sampling site and led to the generation of internal waves with an amplitude of 4 m.
3. The zooplankton community, which was dominated by *Daphnia galeata*, inhabited epilimnetic waters. Downwelling enlarged the thickness of the epilimnetic layer and, hence, led to high zooplankton abundances down to relatively deep water strata indicating lateral transport of zooplankton. As a consequence, area-specific zooplankton abundances increased considerably (max. fourfold) during downwelling.
4. We conclude that classical limnological field sampling, such as for monitoring purposes, can lead to severely biased estimates of zooplankton abundance due to the interfering effects of hydrophysical processes like internal waves.
5. Backscattering strengths measured by a simultaneously deployed Acoustic Doppler Current Profiler (600 kHz) were found to be correlated with estimated zooplankton abundances based on plankton samples.

Keywords: Acoustic Doppler Current Profiler, *Daphnia*, hydrodynamics, internal waves, patchiness

Introduction

Distribution patterns of plankton are known to be patchy as a result of physical and biological processes (Pinel-Alloul *et al.*, 1999; Pinel-Alloul, Methot & Malinsky-Rushansky, 2004). Heterogeneous distributions of zooplankton originate from various processes, some of which can be attributed to internal factors; that is, they are related to the activity and swimming behaviour of the animals (Folt & Burns,

1999). Other causes are linked to external factors, which force organisms to be transported passively, such as by wind-driven currents (George & Edwards, 1976; George & Winfield, 2000). Limnologists have properly documented a number of internal factors inducing spatial heterogeneity including swarming behaviour (Jakobsen & Johnsen, 1987b; Pijanowska & Kowalczewski, 1997), diel vertical and horizontal migrations (Stich & Lampert, 1981; Kvam & Kleiven, 1995), and the active orientation along horizontal and vertical gradients of temperature, food concentration and predation (e.g. Calaban & Makarewicz, 1982; George, 1983; Kvam & Kleiven, 1995; Jakobsen & Johnsen, 1987a; Lampert, McCauley & Manly, 2003).

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In contrast to this, we have a relatively poor understanding of external forcing of spatial heterogeneity. Some studies have highlighted the effect of wind-induced circulation on the horizontal distribution of plankton (George & Edwards, 1976; George & Winfield, 2000). Such wind-induced lateral transport processes were shown to account for 29–47% of basin scale spatial variance of zooplankton (Thackeray *et al.*, 2004). However, wind-driven horizontal transport processes do also have an effect along the vertical axis, through up- or downwelling (George & Edwards, 1976) or the induction of internal waves. Theoretical considerations showed that variations in vertical distribution of plankton as a consequence of internal waves can lead to biased estimates of plankton abundance (Gaedke & Schimmele, 1991). It therefore appears important to test and quantify to what extent such variations in zooplankton vertical distribution really occur in a lake. Although George & Edwards (1976) did not find any direct relationship between wind and vertical patchiness of zooplankton, other studies have indicated that the vertical distribution of zooplankton is affected by wind-induced internal waves (Megard *et al.*, 1997; Easton & Gophen, 2003). Similar interactions between internal waves and zooplankton distribution are known from marine environments (Trevorrow, 1998; McManus *et al.*, 2005). However, a quantitative picture of the hydrodynamic mechanisms at work remained elusive in these investigations. The main objective of our study was, therefore, to investigate the interaction between internal waves and the vertical distribution of zooplankton in combination with a quantitative characterisation of the hydrophysical processes involved therein.

In addition to classical field sampling (e.g. plankton nets), studies on zooplankton distribution often apply other *in situ* techniques for zooplankton detection. Such techniques are either based on optical measurements (e.g. Davis *et al.*, 1992; Sprules *et al.*, 1992) or use hydroacoustics for zooplankton detection (e.g. Schröder & Schröder, 1964; Smith *et al.*, 1992). Hydroacoustic methods are advantageous because they are non-invasive and they deliver data almost instantaneously with a high spatial and temporal resolution (see Schulze, Williamson & Sprules, 1992 and the publications cited therein). It has been successfully shown that lake zooplankton can be efficiently detected by hydroacoustics (Greenlaw, 1979; Gal,

Rudstam & Greene, 1999) and their application in zooplankton distribution studies is well established (Megard *et al.*, 1997; Hembre & Megard, 2003). We therefore also applied hydroacoustic *in situ* detection of zooplankton according to the protocol given in Lorke *et al.* (2004).

This study is designed to measure vertical distribution patterns of zooplankton in combination with a thorough characterisation of the hydrophysical environment by conductivity, temperature and depth profiles (CTD) and by application of an Acoustic Doppler Current Profiler (ADCP). The ADCP measures backscattering signals of suspended particles ('scatterers') and calculates direction and velocity of the scatterers via the Doppler effect. Thus, it provides information about both the vertical distribution of backscattering intensity as a proxy for biological scatterers such as zooplankton and a vertical profile of current velocity and direction. Combining hydrophysical and limnological field techniques provides information to understand how wind-driven forces translate into hydrophysical processes, which finally interact with zooplankton spatial distribution.

Methods

Study site

This study was conducted in Bautzen Reservoir, an impoundment of the river Spree situated in eastern Saxony, Germany (Table 1, Fig. 1). In relation to its large surface area of more than 500 ha the reservoir displays a rather low maximum depth of about 13 m. The Bautzen region is known to be windy and the surroundings of the reservoir do not provide any shelter against strong winds. Consequently, stratification in Bautzen Reservoir is weak and complete

Table 1 Main characteristics of Bautzen Reservoir

Characteristic	Unit	Value
Location		51°13'N, 14°27'E
Trophic state		Eutrophic
Catchment area	km ²	310
Altitude	m a.s.l.	167.5
Surface area	ha	533
Volume	10 ⁶ m ³	39.2
Mean depth	m	7.4
Max. depth	m	13.5
Mean retention time	year	0.45

Fig. 1 Relief map of Bautzen Reservoir. Map coordinates are given as Universal Transverse Mercator coordinates (UTM; zone 33); the white cross denotes the sampling site; m.a.s.l., metres above sea level.

mixing during summer can be observed. Detailed information about the limnological aspects of this reservoir is given elsewhere (Benndorf *et al.*, 2001; Hülsmann, 2003; Wagner *et al.*, 2004). Sampling was conducted in the north-eastern part of the reservoir near the deepest point of the water body (Fig. 1). Water level at the sampling site, during our field survey, was approximately 10 m.

Field survey

The field survey covered a period of 72 h starting from the evening of 5 May 2003. Vertical profiles of temperature, conductivity, pH and oxygen concentration were taken every 90 min using a multi-parameter probe (CTD60; Sea and Sun Technology, Trappenkamp, Germany). Simultaneous vertical profiles of chlorophyll *a* were recorded with a multi-channel fluorescence probe (Fluoroprobe, bbe Moldaenke, Kiel, Germany). The phytoplankton community at that time was dominated by diatoms, mainly *Asterionella formosa* (Hass.) and *Fragilaria crotonensis* (Kitton), and cryptophytes (*Cryptomonas* spp.).

Zooplankton samples were taken with a 5-L water sampler (Limnos.pl, Komorów, Poland), from five depths (one sample per depth; from 0, 3, 5, 8, 10 m, respectively) four times per day at 01:00, 05:30, 13:00 and 20:30 hours (local time), which corresponds to

midnight, sun rise, noon and sunset. Zooplankton was obtained by sieving through a 250- μ m mesh. The zooplankton community was dominated by *Daphnia galeata* (Sars), *Eudiaptomus gracilis* (Sars), and *Cyclops vicinus* (Uljanin). Although the daphnid species that dominated the community in abundance and biomass was morphologically identified as *D. galeata*, enzyme electrophoresis of individuals identified this species as a hybrid between *D. galeata* and *D. hyalina* (*Daphnia galeata* $\times$ *hyalina*, H. Voigt, personal communication). Samples were fixed in sugar formaldehyde according to Haney & Hall (1973) and counted with a stereo microscope in the laboratory. Body lengths of individuals were measured using an image analysis system (SIS, Soft Imaging System GmbH, Münster, Germany) and used to calculate biomass (wet weight) using known length–weight relationships (von Tümppling & Friedrich, 1999).

A 600 kHz Acoustic Doppler Current Profiler (RDI Workhorse ADCP; RD Instruments, USA, <http://www.rdinstruments.com>) was deployed on the bottom facing upward in the vicinity of the sampling site. ADCP measurements provided vertical profiles of current velocities at the sampling site and backscattering intensity as a proxy for zooplankton densities. The ADCP provides no information about taxonomic composition and size distribution of the organisms. A vertical current profile is recorded by the ADCP by means of the Doppler effect in the echo signals of scatterers, which are passively transported and drift with a distinct velocity relative to the ADCP. Hence, returning echo signals display a slightly changed frequency compared with the transmitted signal. The applied ADCP is equipped with four acoustic beams (transducer diameter: 73 mm; beam width: 1.5°), which are tilted by 20° to the vertical axis. Taking into account the prevailing low current velocities within the reservoir the averaging interval of the ADCP was set to 30 min and according to the applied ping rate of 0.33 Hz this resulted in 600 pings per value. A vertical resolution (depth cell size) of 0.5 m was used for data collection and analysis. The centre of the first depth cell was at a depth of 8.3 m, or almost 2 m above the reservoir bottom. The uppermost two depth cells were omitted due to interfering effects of the water surface on the ADCP signals (air bubbles, wave action) resulting in 15 depth cells of usable data per time step. Backscattering intensities (counts) obtained from the ADCP were corrected for absorption by water and

the spreading of the acoustic beam and finally converted to absolute volume backscattering strength (dB) according to Lorke *et al.* (2004). For the comparison of backscattering strength and zooplankton abundance we used the ADCP signal from that depth cell having the largest overlap with the vertical position of the water sampler. Throughout the study period we measured wind direction and velocity 10 m above the ground at an onshore meteorological station (Thies Clima, Göttingen, Germany) approximately 250 m north-east of the sampling site.

For linear regression analysis between ADCP backscatter strength and abundance/biomass of total zooplankton/*Daphnia* a generalised linear model (GLM) with Gamma error distribution and identity link was applied in order to allow for heteroscedasticity. A likelihood ratio test between the fitted GLM and the respective null model was used to test for significance of fitted parameters. Coefficient of determination was calculated as percentage of deviance in the null-model explained by the GLM.

Results

Strong southerly winds with velocities exceeding 10 m s^{-1} occurred during the morning of 6 May (4–9 h; Fig. 2). This wind event, having a relatively long fetch, induced a downwind transport of surface water and resulted in strong downwelling at the sampling site, which reached its maximum deflection at 9:00 hours (Fig. 3). At that time, cold hypolimnetic water was almost completely displaced by downwelling warmer waters. ADCP measurements revealed

Fig. 2 Wind direction (upper panel) and wind velocity (lower panel) during the field survey (5 May to 8 May) measured at a height of 10 m on the shore of Bautzen Reservoir.

Fig. 3 Vertical temperature ($^{\circ}\text{C}$) profiles measured during the field survey (5 May to 8 May) in Bautzen Reservoir.

maximal horizontal currents of about $5\text{--}8 \text{ cm s}^{-1}$ and vertical currents of about $4\text{--}12 \text{ mm s}^{-1}$ (at depths between 2 and 8 m). During the remainder of our survey, wind velocity was weaker and did not exceed 10 m s^{-1} (Fig. 2). Thermal stratification of the water body, during the field survey, was characterised by an almost linear gradient of temperature with depth without a clearly defined thermocline. Isotherms showed large vertical fluctuations with maximum amplitudes exhibited by the 14°C isotherm (Fig. 3). During the downwelling event, the 14°C isotherm indicated a vertical displacement of this water layer of about 6 m over a period of 90 min. Vertical current velocities (downward) during that time reached values between 4 and 12 mm s^{-1} . In the following days vertical oscillations of the isotherms still reached amplitudes of up to 3 m, even during periods with relatively low wind velocities ($<3 \text{ m s}^{-1}$). These oscillations, therefore, cannot be attributed to direct wind effects but rather represent propagating internal waves within the water body. Vertical current velocities during these weaker oscillations were lower and rarely exceeded 4 mm s^{-1} .

Vertical distribution of zooplankton during the field survey was characterised by high abundances in surface layers resulting in a positive correlation between zooplankton abundance and water temperature ($r^2 = 0.40$, $F = 38.06$, d.f. = 58, $P < 0.001$). Residuals of this linear model were unaffected by depth but showed a significant dependency on time since we observed higher zooplankton abundances on the first day than on the following days. However, a multiple linear model with temperature and time as

Table 2 Results of a multiple linear regression model with temperature and time as independent variables and zooplankton abundance as dependent variable

	Estimate	t value	P value
Intercept	571.1	3.16	<0.0001
Temperature	54.6	6.81	<0.0001
Time	33.8	3.11	0.003

The interaction term was identified as not important by AIC. Overall statistics: F statistic: 26.73 on 2 and 57 d.f., $r^2 = 0.48$.

independent variables confirmed temperature to be the dominating factor (Table 2). Chlorophyll concentration showed no distinct vertical distribution pattern and varied between 7 and 10 $\mu\text{g Chl } a \text{ L}^{-1}$. Zooplankton abundance was not correlated with chlorophyll concentration ($r^2 = 0.01$, $F = 0.63$, d.f. = 58, $P = 0.43$). No diurnal vertical migration of zooplankton was observed. However, the vertical distribution of zooplankton was strongly affected by downwelling and internal waves (compare Figs 3 & 4). Individuals were passively transported and did not obviously compensate for vertical displacements created by these hydrophysical processes. During downwelling high zooplankton abundances from the near-surface layers were transported into deeper layers. At the same time zooplankton in the upper layers remained high, suggesting lateral transport of zooplankton towards the sampling site. As a consequence, downwelling increased areal abundance considerably (Fig. 5). Within the 72 h covered by the field survey areal abundance appeared to vary greatly, with maximal abundances being fourfold higher than minimal abundances. When the depth of the 14 °C isotherm is chosen as an indicator of downwelling, a

Fig. 4 Vertical distribution of zooplankton (total abundance of copepods and cladocerans) during the field survey (5 May to 8 May) in Bautzen Reservoir.

Fig. 5 Depth of the 14 °C isotherm and corresponding variation in the area specific abundance of total zooplankton and *Daphnia*.

positive correlation of this depth with areal zooplankton abundance and *Daphnia* abundance, respectively, emerged and accounted for 55% of total variance in areal abundance (Fig. 6).

Backscattering strength measured by the ADCP (Fig. 7) showed a pattern that corresponded to observed zooplankton distributions. Increased zooplankton abundances at greater depths during downwelling on the morning of 6 May were mirrored by stronger backscattering signals (compare Figs 4 & 7). Furthermore, later fluctuations in vertical zooplankton distribution were mirrored by the spatio-temporal patterns in backscattering strengths (compare Figs 4 & 7). Hence, total zooplankton abundance and *Daphnia* abundance, respectively, were significantly correlated with the measured backscattering strength (Fig. 8). Correlation coefficients of similar magnitude were found between backscattering strength and biomass

Fig. 6 Linear regression between depth of the 14 °C isotherm and corresponding area specific abundances of total zooplankton (solid line; $y = 2.1x + 3.6$, $r^2 = 0.55$, $F = 12.03$, d.f. = 10, $P = 0.006$) and *Daphnia* (dashed line; $y = 1.1x + 3.0$, $r^2 = 0.42$, $F = 7.3$, d.f. = 10, $P = 0.02$), respectively.

Fig. 7 Vertical profiles of acoustic backscattering strength (dB) during the field survey (5 May to 8 May) in Bautzen Reservoir. Backscatter data from the surface and bottom layer are not available due to Acoustic Doppler Current Profiler limitations (white areas; see *Methods* for explanation).

Fig. 8 Linear regressions of abundance of total zooplankton (solid line; $y = 11.82x + 1088.8$, $r^2 = 0.68$, $F = 69.7$, d.f. = 34, $P < 0.001$) and *Daphnia* (dashed line; $y = 7.6x + 697.3$, $r^2 = 0.67$, $F = 58.41$, d.f. = 34, $P < 0.001$), respectively, as a function of Acoustic Doppler Current Profiler backscatter strength (generalised linear model with Gamma error distribution and identity link).

of *Daphnia* ($r^2 = 0.63$, $F = 45.51$, d.f. = 34, $P < 0.001$) and total zooplankton ($r^2 = 0.67$, $F = 57.29$, d.f. = 34, $P < 0.001$).

Discussion

The results of our field survey reveal the highly dynamic character and variability of thermal stratification in wind-exposed lakes and reservoirs. By conducting high-resolution measurements of vertical temperature distribution over a period of 72 h we observed wind-driven internal waves with amplitudes of up to 6 m. Such internal waves lead to considerable temporal variation in the thickness of the

epi- and hypolimnion within a short period of time (hours). Areal estimates of zooplankton abundance, characterised by a heterogeneous vertical distribution, are subjected to large fluctuations due to these expanding and contracting water layers. By measuring the abundance of *Daphnia*, which inhabited the warmer epilimnion, we showed areal abundance to vary by a factor of 4 due to internal wave activity. We found that backscattering intensity measured by an ADCP is well correlated with the abundances of total zooplankton and *Daphnia*. Although designed to measure vertical velocity profiles in lakes and oceans, ADCPs also provide information on zooplankton distributions with a high spatial and temporal resolution (Fig. 7 and Lorke *et al.*, 2004).

Our observations show that the distribution of zooplankton in Bautzen Reservoir is patchy. Repeated sampling of the zooplankton community revealed large fluctuations in total zooplankton and *Daphnia* abundance over a period of 72 h due to lateral transport. Variation in population size due to reproduction and mortality can be assumed to be of minor importance within this relatively short period. Instead, internal wave motions, involving fluctuation in the thickness of the epilimnic layer, accounted for 40% and 55% of the total variation in areal *Daphnia* and total zooplankton abundance, respectively.

We found the abundance of *Daphnia* and total zooplankton to be correlated with backscattering intensity with the latter explaining about 70% of the variability observed in zooplankton abundance. Nevertheless, unexplained variability accounts for about 30%, which is still relatively high and could be due to a large number of sources, in part related to sampling techniques and in part for other reasons. Sampling-related errors include errors associated with the net sampling and the differences in volume sampled by the two techniques. Backscattering intensity could potentially be biased by other scatterers besides zooplankton, such as large algal colonies or detritus flocks. However, we also assume that the different averaging time scale associated with the hydroacoustic and classical sampling is a major source of unexplained variability. Whereas the ADCP averaged the measured backscattering intensities over a period of 30 min, the zooplankton samples were depth-specific samples collected within a few minutes.

Alternative techniques for *in situ* detection of zooplankton are provided by optical systems such as

video recording or optical plankton counters (Baumgartner, 2003; Herman, Beanlands & Phillips, 2004). These techniques can also provide information about the size and the shape of zooplankters and preliminary results show good agreement between traditional field sampling methods and plankton counter outputs. However, as this technique is based on shading of an optical signal, only narrow opening windows of a few centimetres can be applied and we do not know the extent to which escape reactions by zooplankters during lowering of the counter system affect the efficiency of detection. In contrast to this, acoustic techniques do not suffer from escape reactions and can sample larger volumes of water.

The need for calibration is common to all *in situ* electronic zooplankton sampling techniques (e.g. acoustic and optical devices). Such calibration requires sampling in close proximity (in time and space) to the area being sampled electronically and will always be necessary as it provides necessary information about the taxonomic composition of the population sampled, which cannot be derived from these *in situ* techniques. However, such acoustic and optical techniques can improve the temporal and spatial resolution of the measurements considerably, enabling the study of processes at finer scales.

Our results have implications for monitoring of lake zooplankton communities. Large fluctuations of zooplankton abundance can be triggered by internal waves or by wind-driven horizontal transport if the lake is exposed to strong winds. Sampling sites situated at a distance from the centre of the lake are especially susceptible to these hydrodynamically caused fluctuations. Such effects may become even stronger in large lakes where internal waves are affected by Coriolis force (Kelvin waves) and induce strong vertical displacements along the shore (Gaedke & Schimmele, 1991). Monitoring programmes in lakes should therefore use information about the hydro-physical environment, such as from temperature profiles or thermistor chains, in order to account for possible effects of internal waves or wind-driven lateral transport processes on the distribution of plankton organisms.

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