The annual cycle of energy input, modal excitation and physical plus biogenic turbulent dissipation in a temperate lake

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1   **Title:** The annual cycle of energy input, modal excitation
2   and physical plus biogenic turbulent dissipation in a temperate lake

3

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10
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12

13 **Key points:**

14

15   **1.** Increased efficiency of atmospheric energy transfer to a lake during stratification
16   when internal seiche modes are active

17

18   **2.** Dissipation measurements in the bottom boundary layer and pycnocline reveal a
19   biogenic component by migrating organisms

20

21 **Abstract**
22 A year of measurements by Doppler Current Profilers, a chain of temperature sensors and a
23 suite of meteorological instruments has been analysed to elucidate the seasonal cycle of the
24 dynamical response of a temperate lake (Windermere) to surface forcing. The efficiency of
25 energy input to the lake (*Eff*) was determined by comparing the rate of working by the surface
26 wind-stress *RWy* with the downward flux of momentum in the atmosphere. *Eff* was found to
27 increase from values of ~0.3% in winter mixed conditions, up to ~1.2% during summer
28 stratification, when internal seiches were present. Water column kinetic energy was similarly
29 enhanced during stratification. Spectral analysis of the axial velocity showed that the first
30 vertical mode was dominant during most of the stratified period with a less prominent second
31 mode appearing in the early part of the summer. The observed periods and vertical structure of
32 these modes generally accorded with estimates from internal wave theory based on density
33 profiles. During stratification, pycnocline dissipation exhibited high variability linked to the
34 surface forcing with an average, depth-integrated, pycnocline dissipation rate of 2.5×10^{-5} W m^{-2}
35 corresponding to ~3-4% of *RWy*. Over the same period, the dissipation rate in the bottom
36 boundary layer (BBL) exhibited a marked diurnal variation unrelated to physical forcing.
37 Acoustic backscatter indicated the presence of vertically migrating organisms with peak
38 aggregation in the BBL around midday coinciding with maximum dissipation. During
39 stratification, biogenic dissipation contributed an average of ~36% of the total BBL dissipation
40 rate of $\sim 5.7 \times 10^{-5}$ W m^{-2}.

41

42 **1. Introduction**
43 The seasonal cycle of stratification in lakes results from the interaction between turbulent
44 mixing, forced mainly by surface wind-stress, and surface heat exchange (Fischer et al., 1979;

45 Imboden and Wüest, 1995). During the spring-summer period, the stratifying effect of surface
46 heat input out-competes vertical mixing, leading to a robust stratified regime developing in all
47 but very shallow polymictic lakes. This stable regime continues until the autumn period, when
48 lakes start to lose heat to the atmosphere and both wind-stress and heat loss act together to
49 erode stratification and induce the autumn overturn. Thereafter a vertically mixed regime
50 prevails through the winter months and continues until surface heat input resumes, around the
51 vernal equinox.

52   The seasonal cycle of stratification and mixing exerts a major influence on lake
53 biogeochemistry and ecology. For example, stable stratification increases the light received by
54 phytoplankton by reducing the depth of the surface mixed layer and separates zones of primary
55 production in the well-lit epilimnion from zones of decomposition in the darker hypolimnion.
56 This decoupling of processes has consequences for nutrient availability in the epilimnion,
57 oxygen depletion in the hypolimnion and consequent phosphorus release from the sediment
58 and the distribution of organisms within a lake (Yankova et al., 2017). When the water column
59 becomes vertically well-mixed during the autumn overturn, much higher mixing rates prevail,
60 and nutrients are rapidly transported up the water column. These changes in the seasonal
61 mixing regime also affects the vertical transfer rate of other scalar properties including, for
62 example, the potent greenhouse gases carbon dioxide and methane (Vachon et al., 2019).

63   The general features of the lacustrine seasonal cycle have long been known, principally
64 on the basis of long-term measurements of the temperature structure. New methods for
65 measuring the internal velocity field and estimating the turbulent kinetic energy dissipation
66 rate, ε, over extended periods using Acoustic Doppler Current Profilers (ADCPs) (Antenucci
67 et al., 2000; Simpson et al., 2011), now offer the prospect of more detailed understanding of
68 the rather subtle interaction of the physical processes involved and their impact on the seasonal
69 cycle of lake biogeochemistry and ecology. In a previous, heuristic study in the south basin of
70 Windermere (Woolway and Simpson, 2017), we used a combination of observations with
71 ADCP and temperature chains to examine the input of energy to the lake and its impact on
72 mixing of the density structure and dissipation in the pycnocline and bottom boundary layer
73 (BBL) for a 55-day period covering the spring transition from a mixed to a stratified water
74 column. Here, we have acquired a new, more extensive series of observations with an extended
75 array of ADCPs covering a period of 416 days in a series of five deployments. We have used
76 this unique data set to document the annual cycle of physical processes in the lake and to make
77 quantitative estimates of key physical parameters controlling the cycle of energy input,
78 dissipation and mixing in the lake.

79   After brief reviews of the observational and analysis methods, which were mostly
80 detailed in Woolway and Simpson (2017), we present the results, starting with an overview of
81 the year-long data set. This is followed by sections based on more detailed analysis of the new
82 data to focus on: (i) determination of the efficiency of energy transfer to the lake by wind stress
83 over the annual cycle, (ii) the changes in the contribution of the internal seiche modes to the
84 response of the lake to wind forcing and (iii) estimates of the levels of energy dissipation and
85 mixing in the pycnocline and the BBL of the lake, both of which exert important controls on
86 lake biogeochemistry.

87
88 **2. Materials and Methods**

2

2.1 Data collection

89   **2.1 Data collection**

90   The measurements which form the basis of our study, were made in the south basin of

91   Windermere (Fig. S1), which is a long ($\sim$10 km) and narrow (width, <1 km) lake basin situated

92   in the English Lake District, with a surface area of $\sim$6.7 km^2, a maximum depth of 42 m, and

93   a mean depth of 16.8 m. Our observations in Windermere covered the period 20th October 2016

94   to 11th December 2017 in a series of five deployments of up to 102 days duration (Table S1).

95   Measurements of water motions and density structure were made with a combination of ADCPs

96   and a chain of temperature sensors moored at the location shown in Fig. S1. The water column

97   observations were complemented by measurements of the wind velocity above the lake surface

98   from a raft-mounted meteorological station located close to the moored instruments near the

99   centre of the lake. Measurements of the water column profile of velocity (Fig. S2) were

100   obtained at the lake centre from a bottom-mounted 600 or 300 kHz ADCP (RDI Workhorse)

101   recording average profiles at intervals of Δt = 120 s based on 50 sub-pings, which were

102   averaged to yield the components of horizontal velocity with a root mean square (rms)

103   uncertainty of $\sim$1 cm s^{-1} and a vertical bin size of Δz = 1 m. The velocity profiles extended

104   from $\sim$2.6 mab (meters above bed) to a level $\sim$3.5 m below the lake surface. A second Doppler

105   Profiler (1 MHz Nortek Signature or 600 kHz RDI Workhorse) was deployed at a depth of 10

106   m to sample the near-surface velocity profile in 0.5 or 1 m bins to $\sim$1.8 m below the surface.

107   Profiles were recorded at 8 Hz in bursts of 175 s at intervals of 2 hours.

108   High precision velocity data for the determination of turbulent dissipation rate, ε, was

109   obtained using fast sampling ADCPs operating in pulse-pulse (p-p) coherent mode which

110   furnishes low noise data (r.m.s $\sim$1 cm s^{-1}) but with a restricted range (Lhermitte and Serafin,

111   1984). Because of the long endurance of the deployments (> 100 days) and heavy storage

112   requirements of the turbulence measurements, the duty cycles of the p-p ADCPs were limited

113   to $\sim$7% of total deployment time. In the BBL, a 1 MHz Nortek Aquadopp profiler, positioned

114   on the lake bed, measured velocity profiles between 0.9 and $\sim$5 mab with a bin size of 10 cm

115   (Fig. S2). Data was recorded at 2 Hz in 512 s bursts at 120-minute intervals. For the

116   determination of dissipation in the pycnocline, a 600 kHz p-p coherent RDI Workhorse (in

117   mode 11), supported by a buoyant collar, was deployed in midwater to measure velocities over

118   a 7 m vertical span with a bin size of 10 cm. Data bursts of 360 s duration, at intervals of 90

119   minutes, were measured at 1 Hz with 2 pings per ensemble. Operation in mid-water of a

120   tethered ADCP supported by a buoyant collar has been validated by comparison with shear

121   probe measurements in a previous study (Lucas et al., 2014). A summary of set-up details for

122   the ADCP instruments is provided in Table S2.

123   The chain of temperature sensors comprised 19 Starmon thermistor microloggers

124   recording every 60 s. The sensors were spaced at intervals of Δz = 2.0 m above 20 m depth and

125   of Δz = 3.0 m below. Temperature data was recorded at a resolution of 0.01 °C and an accuracy

126   of $\sim$0.1 °C. Wind speed and direction were measured at a height of 2.7 m above the lake surface

127   and at time intervals of 240 s by an automatic monitoring station, as described in Woolway and

128   Simpson (2017).

129   In deployment 1, the midwater p-p ADCP failed completely and some of the other data

130   records were terminated early because of battery and data storage limitations. Since the

131   following deployments, 2-5, provided a data return close to 100%, and covered almost the

whole of year 2017, day of year (DOY) 17 to DOY 345, except for breaks of one day for servicing the moorings, we have chosen to treat deployment 1 as our "practice run" and have concentrated the analysis effort on the calendar year 2017.

2.2. Data Analysis

2.2.1. Rate of working by the wind stress

Wind stress inputs energy through the lake surface at a rate which is the product of the stress and the surface velocity. The wind stress components (τ_x, τ_y) acting on the lake surface are determined from the wind observations via the quadratic drag law:

$$(\tau_x, \tau_y) = C_d \rho_a W(U, V) \tag{1}$$

where C_d is the drag coefficient, calculated as a function of wind speed (Large and Pond, 1981); ρ_a is the air density; U and V are the wind components corrected to anemometer height (Large and Pond, 1981); and W is the wind speed. Assuming that the stress is continuous across the air-water interface, the total rate of working RW by the wind stress components, is given by:

$$RW = RW_x + RW_y = \tau_x u + \tau_y v \tag{2}$$

where (u, v) are the near-surface velocity components from the uppermost ADCP bin with valid data. Coordinates are rotated so that τ_y and v are directed along the lake axis. To ensure that RW was not greatly biased by using the velocity measurements from the uppermost ADCP bin, rather than velocity from the immediate surface, we compared the velocity shear in the top five ADCP bins, which occupy a ~2 m layer (Fig. S3). Our comparison suggested that within this sub-surface span, the velocity profile is practically uniform, thus supporting our choice of near-surface velocity in the calculation of RW. However, we do acknowledge that the velocity profile is not necessarily above ~1.9 m depth and, indeed, if one assumes a law of the wall similar to the BBL, the velocity could change rapidly when approaching the lake surface.

To determine the efficiency of energy transfer from the atmosphere to lake we compare RW with the rate of working in a horizontal plane above the lake defined by Lombardo and Gregg (1989) as:

$$P10 = C_d \rho_a \overline{|W^3|} \tag{3}$$

The efficiency of energy transfer, *Eff*, is found by a least squares linear regression of RW on $P10$. Here, the vertical bars indicate the modulus and the overbar denotes the temporal average.

2.2.2. Internal Seiche modes

The periods and modal structure of the internal seiche modes are found by solving the equation for the complex amplitude of the vertical velocity $\psi(z)$ (Gill, 1982):

$$\frac{d^2\psi}{dz^2} + \left(\frac{N^2(z)}{c^2}\right)\psi = 0 \tag{4}$$

174 where $N^2 = -\frac{g}{\rho}\frac{\partial \rho}{\partial z}$ is the buoyancy frequency squared derived from the density profile $\rho(z)$

175 and the boundary condition are $\psi = 0$ at the surface $(z = 0)$ and at the bottom $(z = -h)$.

176 The eigenvalues of this equation for the modes are found numerically following the method of

177 Klink (1999), which are also used to calculate the modal structures $\psi_n(z)$ and the horizontal

178 velocity structure $U_n(z)$. The eigenvalue for mode n is the phase velocity c_n which is used to

179 determine the seiche period $T_n = 2L/c_n$ where L is the "effective length" of the basin, i.e.,

180 the length of a rectangular basin of constant depth. An initial estimate of L was refined by

181 comparing with the seiche period determined independently by spectral analysis.

182

183 *2.2.3. Turbulent Kinetic Energy dissipation rate from high resolution velocity measurements*

184 Time series of turbulent kinetic energy (TKE) dissipation rate, ε, are derived from analysis of

185 the along-beam velocities measured by a p-p coherent ADCP using the Structure Function

186 method (Wiles et al., 2006). The raw, along-beam, velocity components $b(x)$ from each beam

187 are used to estimate a second order structure function defined as:

188

$$D(x,r) = \overline{\left(b'(x) - b'(x+r)\right)^2} \tag{5}$$

190

191 where the overbar indicates the mean over a burst of observations and $b' = b(x) - \overline{b}(x)$ is the

192 fluctuating component of velocity at position z along the beam, such that $D(x,r)$ is the mean-

193 square of the along-beam velocity difference between two points separated by a distance r. For

194 isotropic turbulence, the Kolmogorov hypotheses (Kolmogorov, 1941) anticipate that the

195 structure function $D(x,r)$ is related to the dissipation ε by:

196

$$D(x,r) = C_2 \varepsilon^{2/3} r^{2/3} \tag{6}$$

198

199 where C_2 is a constant, for which laboratory studies indicate a value of $2.0 \pm 15\%$ (Sreenivasan,

200 1995). Linear regression of $D(x,r)$ against $r^{2/3}$ yields:

201

$$D(x,r) = a_0 + a_1 r^{2/3} \tag{7}$$

203

204 where $a_0 = 2\sigma_b^2$ is twice the variance of velocity estimates at a point due to instrumental noise

205 of the ADCP and the gradient a_1 is used to derive an ε estimate as:

206

$$\varepsilon = \left(\frac{a_1}{C_2}\right)^{3/2} \tag{8}$$

208

209 Further details of the Structure Function analysis method are given in Text S1.

210

211 *2.2.4. Seasonal evolution of thermal stratification*

212 As a measure of water column stratification, we use the potential energy anomaly, ϕ (Simpson,

213 1981), defined as:

214

$$\phi = \frac{1}{h}\int_{-h}^{0}\big(\bar{\rho} - \rho(z)\big)gz\,dz \, ; \quad \bar{\rho} = \frac{1}{h}\int_{-h}^{0}\rho(z)\,dz, \qquad (9)$$

where the density profile $\rho(z)$ is derived from temperature data. ϕ is a measure of the energy required (in J m^{-3}) to fully mix the water column; it is zero in mixed conditions and increases with water column stability.

3. Results

3.1 Overview of the observations

To set the context of the results of the subsequent analysis, we show first, in Fig. 1, plots of the principal environmental parameters of the lake, namely the wind forcing, the temperature structure, the profile of axial flow velocity v along the main axis of the lake basin and the water column Kinetic Energy (KE), together with the dissipation measurements in mid-water and in the BBL. Wind forcing (Fig. 1a) is mainly concentrated in short episodes (~1 day) separated by longer periods of relative calm. Wind-stress maxima did not exceed 0.5 Pa except during the exceptional storm Ophelia which occurred immediately after the start of deployment 5 when the peak surface stress was ~1 Pa (Woolway et al., 2018).

There was no pronounced seasonal signal in the wind stress during 2017, although averages of $|\tau|$ over the winter period (deployment 2: 0.0364 Pa) were slightly larger than in spring and summer (deployments 3 and 4: 0.0348 Pa). By contrast, the temperature structure (Fig. 1b), follows the relatively smooth, seasonal pattern expected in dimictic temperate lakes, with mixed conditions in winter giving way to stratification soon after the onset of net surface heat input around the vernal equinox at DOY 79; maximum surface temperature occurs, at or soon after, the summer solstice (DOY 172) with strong stratification persisting beyond the autumn equinox (DOY 265) with the resumption of complete vertical mixing at the autumnal overturn. The profile of axial velocity (Fig. 1c), the profile of velocity along the lake's major axis, exhibits a corresponding seasonal pattern with mostly weak flow during the mixed regime in winter followed by more energetic motions after stratification onset and the associated development of internal seiche modes. These motions have a pronounced vertical structure with flow extending to the surface and bed; the strongest flow and vertical shear are frequently located close to the thermocline which separates warm surface waters from the cooler bottom layers. As the thermocline descends, so does the location of the strongest flows until both approach the lake bed in the autumn overturn when complete vertical mixing resumes.

Over the seasonal cycle there is a marked variation in the water column KE at our central observational site. In Fig. 1d, this variation has been separated into depth-uniform KE_{un} and depth varying KE_{va} components defined as:

$$KE_{un} = \frac{1}{2}\rho h\,\langle v \rangle^2 \, ; \quad KE_{va} = \frac{1}{2}\rho\int_{-h}^{0}(v(z) - \langle v \rangle)^2\,dz \qquad (10)$$

where $\langle v \rangle = \frac{1}{h}\int_{-h}^{0}v(z)\,dz$. During the winter period, when the water column is mixed, these two components are of comparable magnitude but, following the transition to a stratified regime, KE_{va} is considerably increased while KE_{un} is little changed. The mean value of KE_{va} (10.8 J m^{-2}) during the early summer stratified regime in deployment 3 (DOY 95-190) exceeds

257 that for the preceding fully mixed winter period during deployment 2 (DOY 17-94) by a factor
258 of ~7. In the early part of deployment 4, KE_{va} initially continues at a high level but then
259 declines as stratification weakens towards the end of the year.

260   The values of the dissipation rate ε (Fig. 1e-f) are averages over the vertical span of the
261 observations (5-7 m and 3.8 m for the midwater and BBL respectively). The vertical span of
262 the midwater observations was set for deployments 3 and 4 to sample dissipation in the
263 pycnocline during stratified conditions. This strategy was most successful during deployment
264 4 when most of the region of high temperature gradient was covered by the vertical span of the
265 observations. Midwater ε values (Fig. 1e) generally follow the highly variable time course of
266 the wind-stress forcing (Fig. 1a) with a similar pattern of peaks in the two plots. This connection
267 extends through all four deployments shown and is apparent, regardless of whether the water
268 column is stratified or mixed. Midwater ε values range over four decades from the noise level
269 of ~10^{-10} W kg^{-1} to peaks up to 10^{-6} W kg^{-1}.

270   Within the BBL, during deployment 2 when the water column was well-mixed, there
271 was again a considerable degree of matching between peaks in wind-stress and BBL dissipation
272 (Fig. 1f). With the onset of stratification, however, this matching largely disappears and does
273 not return until near the end of deployment 5. During deployments 3 & 4, ε in the BBL
274 exhibited a marked oscillatory form with peak-peak amplitude of up to 10^{-8} W m^{-2}. The origin
275 and significance of this periodic signal is considered in section 3.5.

277 **3.2. Rate of working by the wind stress**
278 We now proceed to determine the rate of mechanical energy input to the lake from the product
279 of the surface stress and the near surface flow, using the approach outlined in section 2.2.1.
280 The wind stress components (τ_x, τ_y), across and along the lake are determined from the
281 quadratic drag law using the wind speed and direction measurements. The surface flow (u_s, v_s)
282 is taken as the velocity, measured by the near-surface doppler in the highest bin with good data
283 (typically 1.6-2.1 m below the lake surface). The axial components of the stress and near
284 surface flow, throughout almost the whole of the year 2017, presented in Fig. 2a-b, are
285 combined to determine their product RW_y, the rate of working in the axial direction. This
286 component dominates over the transverse component RW_x, so that the total $RW \cong RW_y$. For
287 most of the deployment period, RW was positive, i.e., energy is generally being input to the
288 lake flow, with strong positive peaks at times of high wind stress. In the few periods when RW
289 is negative, the surface flow is opposed by the wind stress and KE is being extracted from the
290 lake.

291   We next examine the variation of the efficiency of energy transfer, *Eff*, from the
292 atmosphere to the lake by comparing RW_y to $P10$, the corresponding rate of working by the
293 wind stress above the lake. Notice in Fig. 2c-d that the peaks of RW and $P10$ generally match
294 closely throughout the year but that the magnitude of RW_y, relative to $P10$, increases sharply
295 following the onset of stratification at around DOY 95, while, at the same time, there is an
296 associated marked increase in the magnitude of the near-surface velocities which persists for
297 ~100 days. *Eff* is determined as the slope of a linear, least squares regression of RW_y on $P10$.
298 A series of regressions were performed on 16-day sections of the 2017 data (DOY 17-345)
299 with an overlap of 8 days. The efficiency factor *Eff* plotted in Fig. 2e is the slope of a neutral

7

300 regression (Garrett and Petrie, 1981). Over the annual cycle, *Eff* varies considerably with levels
301 down to ~0.003 (0.3%) during the mixed regime of winter followed by a sharp increase, soon
302 after the onset of stratification, to a maximum of 1.2%. *Eff* values continue to be high (0.6-1%)
303 through the midsummer period until DOY 200, after which, there is a slow decline and a return
304 to low *Eff* levels as the autumn overturn approaches.
305   The occurrence of the rapid rise in *Eff* coinciding with the onset of stratification and the
306 persistence, until the autumn overturn, of higher values than those in winter suggest that *Eff* is
307 being enhanced by the presence of stratification which brings with it the availability of internal
308 seiche modes. However, there is a marked asymmetry in the effect of stratification on *Eff*
309 between the spring and autumn transitions: whereas around DOY 90 a value of $\phi \sim 2.5$ J m^{-3} is
310 enough to trigger the abrupt increase in *Eff*, low values of *Eff* occur for a time after DOY 270,
311 when stratification is still relatively strong ($\phi \sim 20$ J m^{-3}). The weaker influence of stratification
312 on *Eff* in the autumn may result from changes in the vertical structure of stratification. After
313 DOY 245, the pycnocline weakens and moves further away from the surface in an increasingly
314 rapid descent, which increases the thickness of the epilimnion, changes which modify the
315 structure and frequencies of the seiche modes.
316
317 **3.3. Internal seiche modes**
318 In this section, we apply spectral analysis to the velocity profiles from the water column ADCP
319 to determine which internal wave modes are active in the response of the lake and to compare
320 the seasonal progression of the modal frequencies with the results of internal wave theory (Text
321 S2). As explained in section 2.2.2, we employ cross-spectral analysis between each ADCP bin
322 level and a reference level near the bed (bin 2 at ~4 mab) for data sections of 21 days which
323 advance by ~5 days to cover each deployment period. Fig. 3a shows an example of a plot of
324 co-spectrum *Co* versus log (Freq) from all depths from a single 21-day time series (all log
325 values are quoted as log$_{10}$). In this case, the co-spectra reveal the presence of a strong first
326 vertical mode (v1h1) with a single node centred on a frequency of 0.043 ch^{-1}. There is also a
327 clearly defined second vertical mode (v2h1) at a frequency 0.023 ch^{-1} with 2 nodes.
328   To illustrate the variation of the modal contributions over the seasonal cycle, the
329 magnitudes of co-spectra $|Co|$ have been summed over the water column between 3 and 37
330 mab to provide an estimate of the total co-spectral energy at each spectral frequency and time
331 defined as:
332
333 $$CoMS(Freq, t) = \sum_{i=1}^{i=34} |Co(i)| \qquad\qquad (11)$$
334
335 The results for *CoMS* over the whole stratified period are displayed against the log of frequency
336 and time (Fig. 3b). This plot also shows the variation of the frequencies of the first three internal
337 wave modes (v1h1, v2h1 and v3h1) derived from internal wave theory (section 2.2.2) using
338 the square of the buoyancy frequency N^2 based on the density profiles.
339   A high concentration of mode 1 energy occurs early in deployment 3 as stratification
340 develops and a ridge of high energy follows the trend of the theoretical mode 1 frequency to
341 DOY 145. For the rest of deployment 3, the frequency of the peak response falls below the
342 mode 1 frequency and "clings" to the diurnal frequency, arguably, because of enhanced wind

343   forcing at this frequency (Fig. S4). Then after a period of lighter winds (DOY 165-200), mode
344   1 re-appears in deployment 4 with its frequency remaining almost constant and in accord with
345   theory at the semi-diurnal frequency for the first half of the deployment period. Thereafter, a
346   weak ridge declines in frequency, but more slowly than indicated by internal wave theory, an
347   effect which may be due to a reduction in the effective length of the lake as the pycnocline
348   descends, acting to slow the decrease of the seiche period.

349   The second vertical mode also makes a considerable, sustained contribution to the total
350   modal energy from early in deployment 3, when a ridge of energy is seen to follow the
351   theoretical mode 2 frequency into deployment 4 until around DOY 220. After that, there is no
352   clear evidence of mode 2 activity for the rest of the stratified period. As for higher modes, we
353   found no evidence of the excitation of vertical mode 3 or any higher modes contributing
354   significantly to the motion at any time.

355   Following the recovery and re-deployment of the mooring between deployments 4 and
356   5, there was an intense, brief episode of wind forcing during Storm Ophelia which induced a
357   sharp change in the density structure (DOY ~289). There were corresponding reductions in the
358   seiche frequency and amplitude which were apparent in a detailed study by Woolway et al.,
359   (2018), but not resolved in our 21-day spectral analyses. Thereafter, in deployment 5, there was
360   a period of very limited seiche activity which was only partly attributable to reduced wind
361   forcing. The more general decline in seiche activity seems to be the result of changes in
362   stratification as the pycnocline descended rapidly and the epilimnion increased in thickness
363   while the hypolimnion thinned, changes which apparently diminish the generation of seiche
364   motions. After DOY 320, three bouts of stronger wind forcing, in combination with surface
365   cooling, brought about the autumn overturn and seiche motions disappeared.

366

367 **3.4. Turbulent dissipation rate in the pycnocline**
368 The pycnocline is the region of enhanced vertical density gradient between the epilimnion and
369 hypolimnion, which develops as the lake stratifies in spring. It forms initially close to the
370 surface and tends to descend as stratification increases. The development of the pycnocline in
371 the south basin of Windermere during the stratified regime of 2017 is illustrated in Fig. 4a by
372 a contoured plot of N^2 averaged over 24 h. Significant stability gradients ($N^2 > 10^{-4}$ s^{-2}) are
373 seen to develop in the upper half of the water column soon after DOY 95 with a more intense
374 gradient forming just below the surface and descending rapidly to ~25 mab. Thereafter this
375 pycnocline evolves into a slowly deepening, high gradient interface, with N^2 up to
376 2.5×10^{-3} s^{-2}. Between DOY 192 and 275 most of the pycnocline lies within the "pycnocline
377 box", with vertical span $\Delta z = 7$ m, within which ε estimates were determined using velocity
378 measurements from the midwater p-p ADCP. We will use these data to characterise pycnocline
379 ε and its relation to RW.

380   In Fig. 4b-c we show an expanded plot of N^2 in the pycnocline box of deployment 4
381 pycnocline box together with a corresponding depth-time plot of vertical shear squared $Sh^2 =$
382 $\left(\frac{\partial u}{\partial z}\right)^2 + \left(\frac{\partial v}{\partial z}\right)^2$ derived from the pycnocline p-p ADCP velocity data and averaged over 24 h.
383 The colour scales are the same for the two plots so that matching colours would correspond to
384 Richardson number of $Ri = N^2/Sh^2$ of order unity. High gradient regions in N^2 and Sh^2 tend
385 to track each other as they descend over time but the occurrence of high Sh^2 is noticeably more

386　intermittent in time than the rather steady progression of N^2. Since the temperature sensors and
387　the ADCP were separated by ~80 m it is not possible to determine accurately the detail of the
388　space-time distribution of Ri but these average plots of N^2 and Sh^2 indicate a pycnocline in a
389　state of marginal stability in which peaks in shear may trigger mixing events.

390　　　　Figure 5a-b presents the TKE dissipation rate in the pycnocline as $\varepsilon(z,t)$, a function of
391　height in the water column and time and as $\hat{\varepsilon}(t)$ the vertically integrated dissipation rate over
392　the span Δz ~6.6 m of the measurements. The observed $\varepsilon(z,t)$ varies over 4 decades with
393　maxima of up to 1×10^{-6} W kg^{-1}. The vertically integrated dissipation rate reached peaks of
394　$\hat{\varepsilon}$~1.4×10^{-3} W m^{-2} with a mean value in deployment 4 of 2.5×10^{-5} W m^{-2}. Dissipation is seen
395　to be highly intermittent with a time course which is clearly related to RWy, the input of energy
396　at the lake surface (Fig. 5c). A regression of $\hat{\varepsilon}$ on RWy, based on 6 hourly means with zero lag,
397　has a slope of 0.019 ± 0.001 which is highly significant with student's t $=13.4$ and a correlation
398　coefficient 0.56. The corresponding neutral regression slope is 0.034 ± 0.002 which is
399　consistent with the ratio of the means $\bar{\hat{\varepsilon}}/\overline{RWy} = 0.033$. The maximum correlation coefficient
400　occurs for a lag of 2 hours of $\hat{\varepsilon}$ behind RWy, when r $= 0.64$ and the neutral regression slope is
401　0.029 ± 0.0025.

402　　　　During the stratified period of deployment 3, the pycnocline box was restricted to 4.8
403　m in height and less well positioned in relation to the density gradients (Fig. 4) and covers only
404　~50% of the vertical extent of the pycnocline. Allowing for this yields an estimate of the ratio
405　of the means in the stratified period as $\bar{\hat{\varepsilon}}/\overline{RWy} \approx 0.04$, which is not inconsistent with the more
406　robust value from deployment 4. The conclusion from this long, continuous time series of
407　pycnocline dissipation is that only a rather small proportion, ~3-4%, of the surface energy
408　input RWy is, on average, dissipated by turbulence in the pycnocline at the centre of the lake.
409　Most of the dissipation in the pycnocline occurs in short, intense bursts. Within the most
410　energetic of these bursts, the criterion for fully isotropic turbulence (Gargett et al., 1984) is
411　satisfied, i.e. the buoyancy Reynold's number $R_b = \varepsilon/\nu N^2$ is $O(10^2)$ or greater (where ν is the
412　kinematic viscosity). At lower values of R_b, anisotropy will act to modify the dissipation
413　estimates although direct numerical simulations (Smyth and Moum, 2000) suggest that, for the
414　structure function method, the isotropic assumption should remain valid down to values
415　approaching R_b ~1.

416　　　　In principle, spatially resolved profiles of ε and N^2 should permit estimates of the
417　variation of the vertical diffusivity across the pycnocline using the Osborn (1980) relation
418　$K_z = \Gamma\varepsilon/N^2$ with the efficiency of mixing $\Gamma = 0.2$ (Gregg et al., 2018). However, as each
419　estimate of ε uses velocities extending over a span of ±1.9m, the vertical structure is severely
420　smoothed as is evident in Fig. 5. We have, therefore, employed the vertical averages of
421　dissipation $\langle\varepsilon\rangle$ and $\langle N^2\rangle$ in the Osborn relation to estimate the time course of the average
422　diapycnal diffusivity K_z in the pycnocline during deployment 4. The results indicate that
423　mixing in the pycnocline is generally weak except during short-lived maxima of up to K_z ~3
424　$\times10^{-5}$ m^2 s^{-1}. There is an element of uncertainty in the numerical values of K_z here because of
425　the continuing debate about the appropriate value of the mixing efficiency although recent
426　reviews (Gregg et al., 2018, Monismith et al., 2018) support the use of $\Gamma = 0.2$ for the range of
427　Rb in our observations. Note that almost all of the variability in K_z is due to the rapid changes
428　in $\langle\varepsilon\rangle$ which varies over more than 2 orders of magnitude while $\langle N^2\rangle$ (Fig. 5d) declines

429 smoothly from DOY 200 until around DOY 270 when the descending pycnocline starts to exit
430 our pycnocline box. Between DOY 200 and 270, the mean turbulent diffusivity for the period
431 is $\overline{K_z} \approx 10^{-6}$ m^2 s^{-1} which is similar to the value of the kinematic (molecular) viscosity,
432 emphasising the tranquillity of the pycnocline which is stirred significantly only during the
433 infrequent, short bursts of surface forcing.
434
435 **3.5. Turbulent dissipation rate in the BBL**
436 We noted, in section 3.1, the marked difference between the measured dissipation rates in the
437 BBL and that in the pycnocline. While the latter was clearly responding to forcing by the
438 surface stress (Figs 1e, 5), the plots of BBL dissipation rate during much of the stratified
439 summer regime showed elevated levels that were not linked to wind-stress forcing (Fig. 1f). In
440 Fig. 6a-b we show a more detailed comparison of the depth-integrated, measured dissipation
441 rate $\hat{\varepsilon}$ with RWy during deployment 4 when the time courses of the two variables are seen to
442 be largely unrelated. The most striking feature of the dissipation rate time series is a pronounced
443 periodic variation at the diurnal frequency which is evident through much of the deployment
444 and especially prominent after DOY 235. The vertical structure of the dissipation profile $\varepsilon(z,t)$
445 (Fig. 6d) reveals that this diurnal signal is often strongest in the upper part of the dissipation
446 profile and, at times, decreases towards the bottom boundary by more than an order of
447 magnitude (e.g., DOY 258-275). This behaviour is the opposite of what would be expected in
448 a seiche-driven boundary layer, in which dissipation should increase towards the bottom
449 boundary. Moreover, in deployment 4, there is no sign of a persistent seiche of a 48-hour period
450 (see Fig. 7) which would be needed to produce a diurnal variation in dissipation.
451   In search of an explanation for the diurnal modulation of the dissipation rate, we have
452 examined the acoustic backscatter record from the water column ADCP (Fig. 6c) which shows
453 a strong and persistent diurnal pattern characteristic of vertical migration of organisms. Strong
454 backscatter occurs in the upper layers during the hours of darkness and is followed by transfer
455 of the backscattering organisms to the lower half of the water column in time for the daylight
456 hours, when the backscatter signal shows high concentrations extending into the BBL. In order
457 to illustrate the close phase relation between dissipation and the backscatter we show, in Fig.
458 7a-b an expanded section of the backscatter time series together with the average dissipation
459 in the top 5 bins $\langle \varepsilon_5 \rangle$. Maxima in $\langle \varepsilon_5 \rangle$ occur consistently during the daytime when the
460 backscatter signal is high near the bed while minima are apparent in the night-time soon after
461 the upward migration, which can be seen in the vertical velocity w measured by the water
462 column ADCP (Fig. 7c). An upward stream of yellow dots on each diurnal cycle indicates
463 organisms swimming upward with velocities of around 1 cm s^{-1}. The swimmers arrive in the
464 near-surface layers ~4 hours before mid-night (indicated by ticks on time axis) and remain
465 there for ~9.5 hours. The downward return migration is not well resolved in the w plot although
466 there are some indications of downward swimming coinciding with the rapid decline of
467 backscatter in the surface layers, e.g., DOY 244-245.
468   In Fig. 6c there are indications that many, but not all, of the migrators stop in the region
469 of the pycnocline and do not continue further towards the surface. This behaviour is evident in
470 a high concentration band present during night-time which descends from ~28 mab at DOY
471 210 to ~20 mab by DOY 270. This nightly concentration of organisms in the pycnocline, where

472 they are likely to be feeding, is responsible for a biogenic contribution to pycnocline dissipation
473 which, consequently, varies diurnally. In Fig. 7b pycnocline dissipation is plotted (red line)
474 alongside the contemporary BBL dissipation to reveal that the two are in antiphase as the
475 plankton alternate between pycnocline and BBL. This phase relation provides further
476 confirmation of the role of vertical migration in promoting the diurnal variation of dissipation.
477 The calculated dissipation rates were found to be consistent for a range of maximum separation
478 distances, as detailed in the supplementary information (Text S3; Fig. S5-S6), demonstrating
479 that the observed velocity variances are consistent with the Kolmogorov hypotheses for
480 turbulent flows (Kolmogorov, 1941), rather than arising from a non-turbulent source.

481 We now proceed to extrapolate the measured vertical distribution of the BBL
482 dissipation rate to (i) extend the observed ε levels from the lowest measured level down to the
483 lake bed and (ii) estimate the proportion of dissipation which can be attributed to the biogenic
484 component. We shall assume that the physically forced dissipation in the BBL is equal to the
485 TKE production in a law of the wall (LOW) boundary layer (Thorpe, 2005) which is given
486 by $\varepsilon_{LOW}(z) = \frac{\rho u_*^3}{\kappa z}$ (W m^{-3}) where u_* is the friction velocity and κ is the von Karman constant.
487 We shall also assume that, at the lowest level measured ($z_l = 0.96$ mab), the dissipation rate ε_l
488 is primarily due to physical forcing and can be set equal to the LOW value $\varepsilon_l = \frac{\rho u_*^3}{\kappa z_l}$. This
489 second assumption is justified by the rapid decrease in the magnitude of the diurnal (i.e.,
490 'biogenic') component between the highest and lowest Aquadopp bins which can be seen in
491 Fig. 8b. In the second half of the deployment, when the diurnal component is most active, the
492 value in the top bin exceeds that of the lowest bin by 1-2 orders of magnitude.

493 Integrating from z_0, the bedroughness length, to z_l, we have for the additional depth
494 integrated dissipation rate over the water column below the lowest measured bin:

$$\hat{\varepsilon}_{exd} = \int_{z_0}^{z_l} \frac{\rho u_*^3}{\kappa z} dz = \varepsilon_l z_l \ln\left(\frac{z_l}{z_0}\right) \tag{12}$$

498 where $\varepsilon_l = \frac{\rho u_*^3}{\kappa z_l}$ is the observed ε level in the lowest bin. The total depth-integrated dissipation
499 rate in the BBL up to z_u, the height of the highest bin measured, is then:

$$\hat{\varepsilon}_{tot} = \hat{\varepsilon}_{meas} + \hat{\varepsilon}_{exd} \quad [\text{W m}^{-2}] \tag{13}$$

503 where $\hat{\varepsilon}_{meas}$ is the depth integral of the dissipation in the measured bins. The plot of $\hat{\varepsilon}_{tot}$ (Fig.
504 8c) exhibits a reduced diurnal component relative to $\hat{\varepsilon}_{meas}$ (Fig. 8a) because the extrapolated
505 component $\hat{\varepsilon}_{exd}$ is based only on the measurement in the lowest bin where the diurnal
506 component is much weaker. We can also extrapolate upwards from z_l to make an estimate of
507 the dissipation which would occur between z_l and z_u in a LOW boundary layer without inputs
508 from biogenic sources:

$$\hat{\varepsilon}_{exu} = \int_{z_l}^{z_u} \frac{\rho u_*^3}{\kappa z} dz = \varepsilon_l z_l \ln\left(\frac{z_u}{z_l}\right) \tag{14}$$

512   An estimate of the biogenic input between z_l and z_u is then:

514                                   $$\hat{\varepsilon}_{bio} = \hat{\varepsilon}_{meas} - \hat{\varepsilon}_{exu} \tag{15}$$

516   We also have the total physical dissipation in the LOW boundary layer below z_u as:

517                 $$\hat{\varepsilon}_{LOW} = \int_{z_o}^{z_u} \frac{\rho u_*^3}{\kappa z} dz = \varepsilon_l z_l \ln\left(\frac{z_u}{z_0}\right) = \hat{\varepsilon}_{exd} + \hat{\varepsilon}_{exu} \tag{16}$$

520   The result of the extrapolation procedures has been to divide the total BBL dissipation $\hat{\varepsilon}_{tot}$
521   into a physically driven component $\hat{\varepsilon}_{LOW}$ below 4.7 mab (Fig. 8c) and a biogenic
522   component $\hat{\varepsilon}_{bio}$ between 0.9 and 4.7 mab (Fig. 8e).
523   Physically driven dissipation was generally weak as would be expected from the low
524   level of RWy (Fig. 6a) during most of deployment 4. Nevertheless, during the first half of the
525   deployment, $\hat{\varepsilon}_{LOW}$ makes a mostly larger contribution to $\hat{\varepsilon}_{tot}$ than $\hat{\varepsilon}_{bio}$, notably in events like
526   those at DOY 206 and 228 with peaks of ~3.5 x 10^{-4} W m^{-2}, which are clearly linked to wind-
527   stress forcing. By contrast, after DOY 235, $\hat{\varepsilon}_{bio}$ becomes much more active with large diurnal
528   oscillations ranging from peaks of up to ~4.5 x 10^{-4} W m^{-2} down to minima of ~10^{-6} W m^{-2};
529   over the period DOY 240-280, the mean ε_{bio} was ~1.8 x 10^{-5} W m^{-2}. The same extrapolations
530   procedures were applied to the BBL dissipation rate measurements obtained during deployment
531   3 when surface energy input RWy was ~40% higher than during deployment 4. The average
532   depth-integrated dissipation rate components for the two deployments are compared in Table
533   S3. The results for the two deployments are generally rather similar but reflect the higher
534   energy input during deployment 3. Over the combined 200 day period of deployments 3 & 4,
535   the average biogenic dissipation, $\bar{\varepsilon}_{bio}$, amounted to 36% of the total dissipation in the BBL. In
536   the same period, physically-forced dissipation in the BBL was ~4% of RWy, the energy input
537   at the surface by wind-stress.

539   **4. Summary and Discussion**
540   The analysis of the year-long dataset has resulted in the following principal conclusions:

542   i)   The efficiency of mechanical energy transfer from the atmosphere to the lake by
543   wind-stress varies over the seasonal cycle, by a factor of ~4, between a maximum
544   of ~1.2% soon after the onset of stratification and ~0.3% in unstratified conditions.
545   ii)   There is a corresponding cycle in the water column KE with peak values early in
546   the stratified regime greater than those of the mixed regime by a factor of ~7. This
547   increase in KE occurs only in the depth varying component and continues, with a
548   slow decline, until the autumn overturn.
549   iii) There is a well-defined seasonal pattern in the observed frequency of the dominant
550   lowest vertical mode seiche (v1h1) which tracks close to that given by internal wave
551   theory. In the early summer, there was clear evidence of an active second vertical
552   mode (v2h1), whose frequency also follows internal wave theory. There was no
553   evidence of mode 3 or any higher modes being excited.

iv) TKE dissipation rate in the mature summer pycnocline varied widely ($\varepsilon = 10^{-10}$ to 10^{-6} W kg^{-1}) and was closely correlated to surface forcing. On average, total dissipation in the pycnocline accounted for 3-4% of RW_y, while vertical average diffusivity in the pycnocline was limited to maximum values of up to $K_z \sim 3 \times 10^{-5}$ m^{2}s^{-1} occurring in short bursts.

v) Dissipation in the BBL for the summer period was much less influenced by wind stress forcing and exhibited a strong semi-diurnal variation. Acoustic back-scatter data indicated the presence of vertically migrating organisms on a diurnal cycle in which the migrants were present near the bed during the daylight hours when BBL dissipation levels increased by up to two orders of magnitude.

vi) The maximum concentration of organisms in the BBL occurred consistently in phase with the dissipation in the diurnal cycle while measurements of the vertical velocity indicated organisms swimming upward at a velocity of ~1 cm s^{-1} and arriving in the surface layers ~4 hours before midnight.

vii) Many of the swimmers appeared to remain in the pycnocline for several hours where they induced a biogenic contribution to the dissipation rate, which varied diurnally, in phase with the concentration of organisms, and in antiphase with the dissipation rate in the BBL (Fig. 7b).

viii) During the stratified period, the total BBL dissipation rate below 5 m averaged 5.7 x 10^{-5} W m^{-2}, made up of a physical, LOW boundary layer contribution of ~64% with the remaining ~36% coming from biogenic input.

ix) Combined physically-forced dissipation in the pycnocline and the BBL amounted to 5.6-9.0% of RW_y.

The marked change in the efficiency of energy transfer from the atmosphere with the onset of stratification in our observations is consistent, in timing and magnitude, with the abrupt increase in *Eff* observed during the spring transition in 2013 (Woolway and Simpson, 2017). Together with the continuing pattern of enhanced *Eff* through mid-summer 2017 and into the autumn, these findings support the hypothesis that internal seiche modes promote energy transfer during the stratified regime and build the high levels of water column KE observed in summer. Further supportive evidence can be seen in the pattern of modal activity in the stratified period (Fig. 6b) which is similar to that of the variation of *Eff* with a strong response at the onset of stratification and continuing through the mid-summer period before declining in autumn.

It is also probable that the development of a low-friction layer in the pycnocline helps to facilitate the growth of seiches by acting to decouple the epilimnion from the hypolimnion and, thus, promote stronger flows in the surface layer which increases the pycnocline slope which, in turn, forces an enhanced response in the hypolimnion and energises the lake. In late summer, there is a significant decline in *Eff* which may be attributed to a weaker response of pycnocline slope to wind-stress caused by the thickening of the epilimnion as the pycnocline deepens. This mechanism may also explain the weak response of seiche motions during the approach to the autumnal overturn during deployment 5.

596   There are rather few previous reported studies of energy input to lakes and only one, as
597   far as we know, which includes an estimate of *Eff*. On the basis of a series of temperature
598   microstructure measurements in Alpnacher See (Switzerland), Wüest et al., (2000) estimated
599   that, in stratified conditions, ~0.7% of *P10* was dissipated, or used in mixing, below the surface
600   layer (6 m depth), an estimate which is consistent with the average of our estimates for the
601   stratified regime of $\overline{Eff} = 0.70\% \pm 0.23\%$.

602   The spectral analysis of the axial flow in the centre of the lake provides, arguably for
603   the first time, a clear picture of the seasonal progression of modal activity in the velocity field
604   during stratification. The first vertical mode is clearly dominant for most of the time and has a
605   frequency which varies with the evolving stratification in accord with internal wave theory.
606   The first mode response is particularly strong when its frequency is close to that of diurnal
607   wind-stress forcing (Fig. S4). During the early part of the summer, a generally weaker, second
608   vertical mode was also evident at frequencies which again were in accord with theory; no
609   higher modes contributed significantly to the co-spectra. This picture is in broad accord with
610   many previous observations of seiches in temperate lakes comparable to Windermere (Stevens
611   et al., 1996; Lemmin et al., 2005) which mostly show a predominance of the first vertical mode
612   with some additional contribution from the second mode. A clear example of a dominant
613   second vertical mode was observed by Münnich et al., (1992) in the Alpnacher See when there
614   was a substantial metalimnion and the frequency of the second mode matched that of the
615   diurnal wind forcing. One might expect a similar matching to local forcing to promote seiche
616   modes higher than 2, however, the report by Vidal and Casamitjana (2008) of mode 3 seiches
617   in the Sau reservoir (Spain) is one of the few examples in the literature.

618   In spite of the key role of pycnocline dissipation and mixing in the biogeochemistry of
619   lakes, few measurements have been reported in the literature to date. Of these, most have been
620   made using free-fall shear probes and/or temperature microstructure profilers (Imberger and
621   Ivey, 1991; Stevens et al., 2005) both of which are labour intensive and are not suited to long
622   time series of continuous observations. The results of the present study have demonstrated that
623   p-p Doppler profilers, tethered in the pycnocline, combined with Structure Function analysis
624   can provide a straightforward and effective methodology for long term observations of
625   dissipation in all weather conditions. In view of the paucity of existing measurements of TKE
626   dissipation and mixing coefficients in the pycnocline, there would seem to be a strong case for
627   further application of the methods used in this study. Future long-term measurements of this
628   kind might usefully be combined with the complementary approach of Preusse et al., (2010),
629   who used high resolution thermistor chains in Lake Constance to determine pycnocline
630   dissipation via a Thorpe scale analysis of density instabilities.

631   The most surprising results of this study have come from the dissipation rate
632   measurements in the BBL which exhibited a pronounced diurnal variation with ε, at times,
633   increasing with height above the bed. Neither of these features are consistent with dissipation
634   produced by a purely physical process and we have been forced to examine the idea that a
635   component of the dissipation was being driven by diurnal migration of organisms whose
636   presence was clearly indicated by a regular diurnal pattern in the echo-intensity signal from the
637   bottom-mounted ADCP monitoring flow in the water column. Many aquatic organisms
638   perform diurnal vertical migrations for a variety of reasons that trade-off the costs and benefits
639   of conditions in the epilimnion and hypolimnion for metabolic rates, food availability and

predation pressure (Lampert, 1989; Loose & Dawidowitz, 1994). There is a tendency for a greater abundance of fish and zooplankton in surface waters at night and a lesser abundance during the day but there is a large variability of movement patterns depending on species and life stage (Scofield et al. 2020) and some species move horizontally from the pelagic during the night to the littoral at day rather than vertically. Within Windermere, hydroacoustic surveys show that Arctic charr and other fish are more abundant in the surface waters at the night than at the day (Elliott & Baroudy 1992; Winfield & Fletcher 2007). Work on the North Basin of Windermere, which is deeper than the South Basin, in the 1950s (Colebrook, 1960) showed substantial vertical migration for several species of zooplankton. For example, in June 1956, stages IV and V of *Arctodiaptomus laticeps* were below 40 m depth during the day but predominantly above 10 m depth at night. *Eudiaptomus gracilis* was also distributed largely in the top 10 m at night but showed lesser and variable migration to depth during the day depending on stage and sex. In another campaign in autumn 1955, *Cyclops strenuous* males also performed diurnal vertical migration, being absent from the surface during the day while accumulating between 15 and 30 m depth. Thus, the well-known patterns of diurnal vertical migration of fish and especially zooplankton, that also occur in Windermere, are consistent with the acoustic backscatter data shown in our study. The estimated rates of swimming are also consistent with measured swimming speeds of zooplankton which can exceed 1 cm s^{-1} depending on species and conditions (Ekvall et al. 2020).

The close phase relation between the BBL dissipation rate and the echo signal with maximum dissipation occurring when migrators were present in the BBL, strongly supports the hypothesis that migrating organisms were contributing to BBL dissipation. Further support comes from the pycnocline measurements which indicate a diurnally varying, biogenic component which varies in antiphase with the BBL dissipation rate. A first-order separation of the biogenic and physical sources of dissipation in the BBL, obtained by extrapolating downwards and upwards from the lowest Doppler bin using the law of the wall, indicated that the biogenic component accounted for an average of ~36% of the total BBL dissipation rate during the stratified regime.

Biogenic mixing in the ocean has been widely reported in the literature, but there are only a few studies related to mixing in lakes (Noss and Lorke, 2014; Simoncelli et al., 2017; Simoncelli et al., 2018). The only report of measured values of biogenic dissipation in the lacrustine environment is, as far as we know, the recent paper of Sepulveda Steiner et al., (2021) who observed a 1 m-thick mixed-layer driven by bioconvection due to vertically migrating bacteria in a stratified lake. Our serendipitous observations of a very different bio-turbulence scenario, in Windermere, will, we trust, stimulate further investigations of bio-turbulence in lakes, where the generally low levels of physically-driven turbulence, can make modest biogenic inputs, of the type we have observed, important in promoting mixing. There are some obvious limitations in our study which was planned to investigate only physical aspects of the seasonal cycle, so there was no net sampling of the plankton to establish the plankton species involved and their behaviour. From past sampling programmes in Windermere (as described above), it seems likely that the zooplankton responsible for generating the biogenic contribution to turbulent dissipation, which we have observed, are copepods of unknown species. It is their swimming activity which generates the bio-turbulence but their regular

vertical migration which strongly modulates turbulence levels in the BBL and, to a lesser degree, in the pycnocline, which provided us with a helpful guide to their presence and activity.

There is also an interesting question about whether the scales of turbulence, produced by swimming zooplankton swimming, are too small to bring about significant mixing. In experiments with large concentrations of zooplankton in laboratory tanks, Houghton et al., (2018) have demonstrated that migrating aggregations of organisms can produce large-scale mixing eddies as a result of flow, in the wakes of individual organisms, coalescing to form a large-scale downward jet during upward swimming, even in the presence of a strong density stratification. Our observations, which rely on the structure function determination of turbulent velocity differences over scales greater than 2 bins (20 cm), also suggest that such relatively large-scale eddies are indeed produced by zooplankton stirring. This conclusion is further supported by trial evaluations of ε for a range of r_{max} values between 1 and 3 m which indicates minimal dependence on the maximum separation distance (Text S3; Fig. S5).

References

Antenucci, J.P., Imberger, J. & Saggio, A. (2000). Seasonal evolution of the basin-scale internal wave field in a large stratified lake. *Limnol. Oceanogr.* 45, 1621–1638

Colebrook, J.M. (1960). Plankton and water movements in Windermere. *Journal of Animal Ecology* 29(2), 217-240

Ekvall, M. et al. (2020). Behavioural responses to co-occurring threats of predation and ultraviolet radiation in Daphnia. *Freshwater Biol* 65, 1509-1517

Elliott, J.M. & Baroudy, E. (1992), Long-term and short-term fluctuations in the numbers and catches of Arctic charr, Salvelinus alpinus (L.), in Windermere (northwest England). *Annls Limnol.* 28, 135-146

Fischer, H.B., List, E. J., Koh, R. C. Y., Imberger, J. & Brooks, N.H. (1979). Mixing in Inland and Coastal Waters. Academic Press, London.

Gargett A.C., Osborn, T.R. & Nasmyth, P.W. (1984). Local isotropy and the decay of turbulence in a stratified fluid. *J. Fluid Mech.*144, 231-280

Garrett, C., Petrie, B. (1981). Dynamical aspects of the flow through the strait of Belle Isle. *J. Phys. Oceanogr.* 11, 376-393.

Gill, A.G. (1982). Atmosphere-ocean dynamics. *Int. Geophys. Ser.* 30, 159–162.

Gregg, M.C. et al. (2018). Mixing efficiency in the ocean. Annual Review of Marine Science 10, 443-473.

726   Houghton, I.A., Koseff, J.R., Monismith, S.G., Dabiri, J.O. (2018). Vertically migrating
727   swimmers generate aggregation-scale eddies in a stratified column. *Nature*. 556, 497–
728   500

729   Imberger, J. & Ivey, G.N. (1991). On the nature of turbulence in a stratified fluid. Part II:
730   Application to lakes. *J. Phys. Oceanogr.* 21, 659–680.

731   Imboden, D.M. & Wüest, A. (1995). Mixing mechanisms in lakes. In: Physics and chemistry
732   of Lakes. Springer, pp 83–138.

733   Klink, J. (1999). Dynmodes.m—ocean dynamics vertical modes. Woods Hole (MA): Woods
734   Hole Science Center, SEA-MAT, Matlab tools for oceanographic analysis. Available
735   from: http://woodshole.er.usgs.gov/operations/sea-mat/index.html

736   Kolmogorov, A.N. (1941). Dissipation of energy in the locally isotropic turbulence. *Dokl.*
737   *Akad. Nauk SSSR*, 32, 19-21

738   Lampert, W. (1989). The Adaptive Significance of Diel Vertical Migration of Zooplankton.
739   *Functional Ecology* 3, 21-27

740   Large, W.G. & Pond, S.S. (1981). Open ocean momentum flux measurements in moderate to
741   strong winds. *J. Phys. Oceanogr.* 11, 324–336

742   Lemmin, U., Mortimer, C.H., Bäuerle, E. (2005). Internal seiche dynamics in Lake Geneva.
743   *Limnol. Oceanogr.* 50(1), 207-216

744   Lhermitte, R. & Serafin, R. (1984). Pulse-to-pulse coherent Doppler sonar signal processing
745   techniques. *J. Atmos. Oceanic Technol.* 1, 293–308.

746   Lombardo, C.P. & Gregg, M.C. (1989). Similarity scaling of viscous and thermal dissipation
747   in a convecting surface boundary layer. *J Geophys. Res-Oceans* 94, 6273–6284.

748   Loose, C.J. & Dawidowitz, P. (1994), Trade-Offs in Diel Vertical Migration by Zooplankton:
749   The Costs of Predator Avoidance. *Ecology* 75(8), 2255-2263

750   Lucas, N., Simpson, J.H., Rippeth, T.P. & Old, C. (2014). Measuring dissipation via the
751   structure function using a tethered ADCP. *J Atmos. Oceanic Technol.* 31, 1826–1837

752   Monismith, S.G., Koseff, J.R. & White, B.L. (2018). Mixing efficiency in the presence of
753   stratification: When is it constant? *Geophys. Res. Lett.* **45**, 5627–5634

754   Münnich, M.A., Wüest, A. & Imboden, D.M. (1992). Observations of the second vertical mode
755   of the internal seiche in an alpine lake. *Limnol. Oceanogr.* 37, 1705–1719. doi:10.4319/
756   lo.1992.37.8.1705

757   Noss, C. & Lorke, A. (2014). Direct observation of biomixing by vertically migrating
758   zooplankton. *Limnol. Oceanogr.* 59(3), 724-732.

759   Osborn, T. R. (1980). Estimates of the local rate of vertical diffusion from dissipation
760   measurements. *J. Phys. Oceanogr.* 10, 83-89.

761   Preusse, M., Peeters, F. & Lorke, A. (2010). Internal waves and the generation of turbulence
762   in the thermocline of a large lake. *Limnol. Oceanogr.* 55(6), 2353– 2365.

763   Scofield, A.E. et al. (2020). Heterogeneity in zooplankton distributions and vertical migrations:
764   Application of a laser optical plankton counter in offshore Lake Michigan. *J. Great*
765   *Lakes* Res 46(4), 780-797

766   Simoncelli, S., Thackeray S. & Wain, D. (2017). Can small zooplankton mix lakes? *Limnol.*
767   *Oceanogr. Lett.* 2(5):167–176.

768   Simoncelli, S., Thackeray, S.J., Wain, D.J. (2018). On biogenic turbulence production and
769   mixing from vertically migrating zooplankton in lakes. *Aquat. Sci.* 80:35.

770 Simpson, J.H. (1981). The shelf-sea fronts: Implications of their existence and behaviour.
771   *Philos. Trans. R. Soc. Lond*. 302, 531–546. doi:10.1098/rsta.1981.0181

772 Simpson, J.H., Wiles, P.J. & Lincoln, B.J. (2011). Internal seiche modes and bottom boundary-
773   layer dissipation in a temperate lake from acoustic measurements. *Limnol. Oceanogr.*
774   56, 1893–1906. doi:10.4319/lo. 2011.56.5.1893

775 Smyth, W.D. & Moum, J.N. (2000). Anisotropy of turbulence in stably stratified mixing layers.
776   *Phys. Fluids*. 12(6), 1343-1362.

777 Sreenivasan, K.R. (1995). On the universality of the Kolmogorov constant. *Phys. Fluids*. 7,
778   2778-2784

779 Sepúlveda Steiner, O., Bouffard, D. & Wüest, A. (2021), Persistence of bioconvection-induced
780   mixed layers in a stratified lake. Limnol Oceanogr. https://doi.org/10.1002/lno.11702

781 Stevens C.L., Fisher T.S.R. & Lawrence G.A. (2005). Turbulent layering beneath the
782   pycnocline in a strongly stratified pit lake. *Limnol. Oceanogr.*, 50(1), 197–206.

783 Stevens, C., Lawrence, G., Hamblin, P. & Carmack, E. (1996). Wind forcing of internal waves
784   in a long narrow stratified lake. *Dyn. Atmos. Oceans*, 24, 41–50

785 Thorpe, S.A. (2005). The Turbulent Ocean, Cambridge University Press.

786 Vachon, D. et al. (2019). Influence of water column stratification and mixing patterns on the
787   fate of methane produced in deep sediments of a small eutrophic lake. *Limnol.*
788   *Oceanogr.* 64(5):2114-2128.

789 Vidal, J. & Casamitjana, X. (2008). Forced Resonant Oscillations as a Response to Periodic
790   Winds in a Stratified Reservoir. *J. Hydraul. Eng*. 134(4), 416-425.

791 Wiles P.J., Rippeth, T.P., Simpson, J.H. & Hendricks, P.J. (2006). A novel technique for
792   measuring the rate of turbulent dissipation in the marine environment. *Geophys. Res.*
793   *Lett*. 33: L21608. doi:10.1029/2006GL027050.

794 Winfield, I.J., Fletcher, J.M. & James, J.B. (2007). Seasonal variability in the abundance of
795   Arctic charr (Salvelinus alpinus (L.)) recorded using hydroacoustics in Windermere,
796   UK and its implications for survey design. *Ecology of Freshwater Fish* 16(1), 64-69

797 Woolway, R.I. & Simpson, J.H. (2017). Energy input and dissipation in a temperate lake during
798   the spring transition. *Ocean Dynamics* 67, 959–971. doi 10.1007/s10236-017-1072-1

799 Woolway, R.I., Simpson, J.H., Spiby, D., Feuchtmayr, H., Powell, B. & Maberly, S.C. (2018).
800   Physical and chemical impacts of a major storm on a temperate lake: a taste of things
801   to come? *Climatic Change* 151, 333-347. doi: 10.1007/s10584-018-2302-3.

802 Wüest, A., Piepke, G., Van Senden, D.C. (2000). Turbulent kinetic energy balance as a tool for
803   estimating vertical diffusivity in wind-forced stratified waters. *Limnol. Oceanogr*. 45,
804   1388–1400. doi:10.4319/lo.2000.45.6.1388

805 Yankova, Y. et al., (2017). Abrupt stop of deep water turnover with lake warming: Drastic
806   consequences for algal primary producers. *Sci. Rep*. **3**:13770

807 **References from Supporting Information**
808 Emery, W.J. & Thomson, R.E. (1998). Data analysis methods in physical oceanography.
809   *Oceanographic Literature Review* 1, 45.
810 Scannell, B., Rippeth, T.P., Simpson, J.H., Polton, J.A. & Hopkins, J.E. (2017). Correcting
811   Surface Wave Bias in Structure Function Estimates of Turbulent Kinetic Energy
812   Dissipation Rate. *J. Atmos. Oceanic Technol.* 34, 2257-2273
813 Ramsbottom, A.E. (1976). Depth charts of the Cumbrian Lakes. *Freshw. Biol. Assoc. Sci. Publ.*
814   33

858   to 36 metres above bed (mab) **(d)** Vertical structure of the dissipation rate $\varepsilon(z,t)$ (W kg^{-1}) in
859   the BBL. Black rectangle shows the 7-day period of the expanded region in Fig. 7.

860

861   **Figure 7**. Expanded plots for day of year (DOY) 240-247 of **(a)** the acoustic backscatter
862   intensity, BS from the water column ADCP (black box in Fig. 6) relative to metres above bed
863   (mab), **(b)** the mean dissipation (W kg^{-1}) in the top five Aquadopp bins $\langle \varepsilon_5 \rangle$ (blue) and in the
864   pycnocline $\langle \varepsilon_{pyc} \rangle$ (red), and **(c)** the vertical velocity w (m s^{-1}) from the water column ADCP.
865   Note that on the time axis, the larger ticks denote the times of midnight (UT).

866

867   **Figure 8**. Extrapolation of dissipation in the bottom boundary layer (BBL). **(a)** $\hat{\varepsilon}_{meas}$ the
868   integrated measured dissipation between 0.96 and 4.66 metres above bed (mab) in the BBL.
869   **(b)** ε_{bin} : dissipation rate (W kg^{-1}) in the highest bin (red, 4.66 mab) and in the lowest bin
870   (black, 0.96 mab) of the Aquadopp span. **(c)** $\hat{\varepsilon}_{tot} = \hat{\varepsilon}_{meas} + \hat{\varepsilon}_{exd}$: total dissipation in the
871   BBL up to 4.66 mab. **(d)** $\hat{\varepsilon}_{LOW} = \hat{\varepsilon}_{exd} + \hat{\varepsilon}_{exu}$: estimate of physical dissipation in the BBL up
872   to 4.66 mab. **(e)** $\hat{\varepsilon}_{bio} = \hat{\varepsilon}_{meas} - \hat{\varepsilon}_{exu}$ estimate of the biogenic component of dissipation
873   between 0.96 mab and 4.66 mab.

dep 2   dep 3   dep 4   dep 5

(a)

0.95

(b)

(c)

(d)

(e)

(f)

DOY 2017

(a)

(b)

(c)