

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

4 **Authors:** John H. Simpson¹, R. Iestyn Woolway², Brian Scannell¹,
5 Martin J. Austin¹, Ben Powell¹, Stephen C. Maberly³
6

7 **Affiliations:**

- 8 1. Bangor University, School of Ocean Sciences, Menai Bridge, Anglesey, UK
- 9 2. European Space Agency Climate Office, ECSAT, Harwell Campus, Didcot,
10 Oxfordshire, UK
- 11 3. UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, UK

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 RW_y with the downward flux of momentum in the atmosphere. *Eff* was found to
27 increase from values of $\sim 0.3\%$ in winter mixed conditions, up to $\sim 1.2\%$ 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 $2.5 \times 10^{-5} \text{ W m}^{-2}$
35 corresponding to $\sim 3\text{-}4\%$ of RW_y . 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 $\sim 36\%$ of the total BBL dissipation
40 rate of $\sim 5.7 \times 10^{-5} \text{ W m}^{-2}$.

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**

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 (~ 10 km) and narrow (width, < 1 km) lake basin situated
92 in the English Lake District, with a surface area of ~ 6.7 km², 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 $\Delta t = 120$ 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 ~ 1 cm s⁻¹ and a vertical bin size of $\Delta z = 1$ m. The velocity profiles extended
104 from ~ 2.6 mab (meters above bed) to a level ~ 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 ~ 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 ~ 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 ~ 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 $\Delta z = 2.0$ m above 20 m depth and
125 of $\Delta z = 3.0$ m below. Temperature data was recorded at a resolution of 0.01 °C and an accuracy
126 of ~ 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

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

135

136 **2.2. Data Analysis**

137 *2.2.1. Rate of working by the wind stress*

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

141

$$142 \quad (\tau_x, \tau_y) = C_d \rho_a W(U, V) \quad (1)$$

143

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

148

$$149 \quad RW = RW_x + RW_y = \tau_x u + \tau_y v \quad (2)$$

150

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

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

$$163 \quad P10 = C_d \rho_a \overline{|W^3|} \quad (3)$$

164

165 The efficiency of energy transfer, Eff , is found by a least squares linear regression of RW on
 166 $P10$. Here, the vertical bars indicate the modulus and the overbar denotes the temporal average.

167

168 *2.2.2. Internal Seiche modes*

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

171

$$172 \quad \frac{d^2 \psi}{dz^2} + \left(\frac{N^2(z)}{c^2} \right) \psi = 0 \quad (4)$$

173

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

$$189 \quad D(x, r) = \overline{(b'(x) - b'(x + r))^2} \quad (5)$$

190

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

$$197 \quad D(x, r) = C_2 \varepsilon^{2/3} r^{2/3} \quad (6)$$

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

$$202 \quad D(x, r) = a_0 + a_1 r^{2/3} \quad (7)$$

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

$$207 \quad \varepsilon = \left(\frac{a_1}{C_2}\right)^{3/2} \quad (8)$$

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

$$215 \quad \phi = \frac{1}{h} \int_{-h}^0 (\bar{\rho} - \rho(z)) g z dz; \quad \bar{\rho} = \frac{1}{h} \int_{-h}^0 \rho(z) dz, \quad (9)$$

216

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

220

221 3. Results

222 3.1 Overview of the observations

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

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

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

250

$$251 \quad KE_{un} = \frac{1}{2} \rho h \langle v \rangle^2; \quad KE_{va} = \frac{1}{2} \rho \int_{-h}^0 (v(z) - \langle v \rangle)^2 dz \quad (10)$$

252

253 where $\langle v \rangle = \frac{1}{h} \int_{-h}^0 v(z) dz$. During the winter period, when the water column is mixed, these
 254 two components are of comparable magnitude but, following the transition to a stratified
 255 regime, KE_{va} is considerably increased while KE_{un} is little changed. The mean value of KE_{va}
 256 (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 $\sim 10^{-10}$ 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.

276

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

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 $\phi \sim 2.5 \text{ J m}^{-3}$ 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 ($\phi \sim 20 \text{ J m}^{-3}$). 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 $\sim 4 \text{ mab}$) 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 $\log(\text{Freq})$ 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

$$333 \quad CoMS(\text{Freq}, t) = \sum_{i=1}^{i=34} |Co(i)| \quad (11)$$

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 ($N^2 > 10^{-4} \text{ s}^{-2}$) 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 $2.5 \times 10^{-3} \text{ s}^{-2}$. Between DOY 192 and 275 most of the pycnocline lies within the “pycnocline
377 box”, with vertical span $\Delta z = 7 \text{ m}$, 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 $\Delta z \sim 6.6$ 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 $\hat{\varepsilon} \sim 1.4 \times 10^{-3}$ 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 $\sim 50\%$ 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, $\sim 3\text{-}4\%$, 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 $R_b \sim 1$.

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 ± 1.9 m, 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 $K_z \sim 3$
 424 $\times 10^{-5}$ 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 R_b 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 $\overline{K_z} \approx 10^{-6} \text{ m}^2 \text{ s}^{-1}$ 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 $\hat{\epsilon}$ with RW_y 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 $\epsilon(z, t)$
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 ($\langle \epsilon_5 \rangle$). Maxima in $\langle \epsilon_5 \rangle$ 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:

$$495 \quad \hat{\varepsilon}_{exd} = \int_{z_0}^{z_l} \frac{\rho u_*^3}{\kappa z} dz = \varepsilon_l z_l \ln\left(\frac{z_l}{z_0}\right) \quad (12)$$

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

$$498 \quad \hat{\varepsilon}_{tot} = \hat{\varepsilon}_{meas} + \hat{\varepsilon}_{exd} \quad [\text{W m}^{-2}] \quad (13)$$

499 where $\hat{\varepsilon}_{meas}$ is the depth integral of the dissipation in the measured bins. The plot of $\hat{\varepsilon}_{tot}$ (Fig.
 500 8c) exhibits a reduced diurnal component relative to $\hat{\varepsilon}_{meas}$ (Fig. 8a) because the extrapolated
 501 component $\hat{\varepsilon}_{exd}$ is based only on the measurement in the lowest bin where the diurnal
 502 component is much weaker. We can also extrapolate upwards from z_l to make an estimate of
 503 the dissipation which would occur between z_l and z_u in a LOW boundary layer without inputs
 504 from biogenic sources:

$$505 \quad \hat{\varepsilon}_{exu} = \int_{z_l}^{z_u} \frac{\rho u_*^3}{\kappa z} dz = \varepsilon_l z_l \ln\left(\frac{z_u}{z_l}\right) \quad (14)$$

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511

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

513

$$514 \hat{\epsilon}_{bio} = \hat{\epsilon}_{meas} - \hat{\epsilon}_{exu} \quad (15)$$

515

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

517

$$518 \hat{\epsilon}_{LOW} = \int_{z_o}^{z_u} \frac{\rho u_*^3}{\kappa z} dz = \epsilon_l z_l \ln\left(\frac{z_u}{z_o}\right) = \hat{\epsilon}_{exd} + \hat{\epsilon}_{exu} \quad (16)$$

519

520 The result of the extrapolation procedures has been to divide the total BBL dissipation $\hat{\epsilon}_{tot}$
521 into a physically driven component $\hat{\epsilon}_{LOW}$ below 4.7 mab (Fig. 8c) and a biogenic
522 component $\hat{\epsilon}_{bio}$ between 0.9 and 4.7 mab (Fig. 8e).

523

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

538

539 4. Summary and Discussion

540 The analysis of the year-long dataset has resulted in the following principal conclusions:

541

- 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 $\sim 1.2\%$ soon after the onset of stratification and $\sim 0.3\%$ 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.

- 554 iv) TKE dissipation rate in the mature summer pycnocline varied widely ($\epsilon = 10^{-10}$ to
555 10^{-6} W kg⁻¹) and was closely correlated to surface forcing. On average, total
556 dissipation in the pycnocline accounted for 3-4% of RW_y , while vertical average
557 diffusivity in the pycnocline was limited to maximum values of up to
558 $K_z \sim 3 \times 10^{-5}$ m²s⁻¹ occurring in short bursts.
- 559 v) Dissipation in the BBL for the summer period was much less influenced by wind
560 stress forcing and exhibited a strong semi-diurnal variation. Acoustic back-scatter
561 data indicated the presence of vertically migrating organisms on a diurnal cycle in
562 which the migrants were present near the bed during the daylight hours when BBL
563 dissipation levels increased by up to two orders of magnitude.
- 564 vi) The maximum concentration of organisms in the BBL occurred consistently in
565 phase with the dissipation in the diurnal cycle while measurements of the vertical
566 velocity indicated organisms swimming upward at a velocity of ~ 1 cm s⁻¹ and
567 arriving in the surface layers ~ 4 hours before midnight.
- 568 vii) Many of the swimmers appeared to remain in the pycnocline for several hours
569 where they induced a biogenic contribution to the dissipation rate, which varied
570 diurnally, in phase with the concentration of organisms, and in antiphase with the
571 dissipation rate in the BBL (Fig. 7b).
- 572 viii) During the stratified period, the total BBL dissipation rate below 5 m averaged 5.7
573 $\times 10^{-5}$ W m⁻², made up of a physical, LOW boundary layer contribution of $\sim 64\%$
574 with the remaining $\sim 36\%$ coming from biogenic input.
- 575 ix) Combined physically-forced dissipation in the pycnocline and the BBL amounted
576 to 5.6-9.0% of RW_y .

577

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

588 It is also probable that the development of a low-friction layer in the pycnocline helps to
589 facilitate the growth of seiches by acting to decouple the epilimnion from the hypolimnion and,
590 thus, promote stronger flows in the surface layer which increases the pycnocline slope which,
591 in turn, forces an enhanced response in the hypolimnion and energises the lake. In late summer,
592 there is a significant decline in Eff which may be attributed to a weaker response of pycnocline
593 slope to wind-stress caused by the thickening of the epilimnion as the pycnocline deepens. This
594 mechanism may also explain the weak response of seiche motions during the approach to the
595 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 E_{ff} . 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, $\sim 0.7\%$ of P_{10} 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 $\overline{E_{ff}} = 0.70\% \pm 0.23\%$.

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

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

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

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

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

685 There is also an interesting question about whether the scales of turbulence, produced
686 by swimming zooplankton swimming, are too small to bring about significant mixing. In
687 experiments with large concentrations of zooplankton in laboratory tanks, Houghton et al.,
688 (2018) have demonstrated that migrating aggregations of organisms can produce large-scale
689 mixing eddies as a result of flow, in the wakes of individual organisms, coalescing to form a
690 large-scale downward jet during upward swimming, even in the presence of a strong density
691 stratification. Our observations, which rely on the structure function determination of turbulent
692 velocity differences over scales greater than 2 bins (20 cm), also suggest that such relatively
693 large-scale eddies are indeed produced by zooplankton stirring. This conclusion is further
694 supported by trial evaluations of ε for a range of r_{max} values between 1 and 3 m which indicates
695 minimal dependence on the maximum separation distance (Text S3; Fig. S5).

696

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706

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815 List of Figures

816

817 **Figure 1.** Overview of observations in deployments 2 to 5 in Windermere during the 2017
818 campaign. **(a)** Wind stress magnitude τ (Pa); **(b)** Temperature ($^{\circ}\text{C}$); **(c)** Water column velocity
819 v , measured between ~ 3 metres above bed (mab) and ~ 37 mab; **(d)** Water column kinetic
820 energy (KE) components: KE_{un} (black) and KE_{va} (red), based on the depth-average and depth-
821 varying axial velocity, respectively; **(e)** Depth-mean dissipation rate (W kg^{-1}) measured in a
822 vertical span of 6.6 m (4.9 m in deployment 3); span depth was located in the pycnocline during
823 the stratified regime (deployments 3 and 4); **(f)** Depth-mean dissipation rate (W kg^{-1}) in the
824 bottom boundary layer (BBL) between 0.96 and 4.66 mab.

825

826 **Figure 2.** Rate of working and efficiency of energy transfer, Eff , through the lake surface. **(a)**
827 axial wind-stress τ (Pa); **(b)** near-surface axial velocity v_s (m s^{-1}) measured at 1.6-2.1 m below
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833

834 **Figure 3.** Spectral analysis of internal wave motions. **(a)** Co-spectrum between axial velocity
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837 show the variation of modal frequencies based on internal wave theory with observed density
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839 diurnal and semi-diurnal periods. The Co-spectrum is the in-phase component of the Cross-
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841

842 **Figure 4.** Pycnocline structure and shear. **(a)** Contours of daily means of N^2 (s^{-2}) derived from
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845 deployment 4 pycnocline box. **(c)** Corresponding plot of Sh^2 (s^{-2}) derived from pycnocline p-
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847

848 **Figure 5.** Dissipation (ε) and diffusivity (K_z) in the pycnocline during deployment 4. Log plots
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852 **(d)** Stability frequency squared $N^2(\text{s}^{-2})$; **(e)** Vertical diffusivity K_z ($\text{m}^2 \text{s}^{-1}$).

853

854 **Figure 6.** Bottom boundary layer (BBL) dissipation and echo intensity during deployment 4.
855 **(a)** Rate of energy input at the lake surface RW_y (W m^{-2}); **(b)** Depth integrated, measured
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857 Backscatter intensity, BS (dB) from bottom mounted ADCP covering water column from 3.7

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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
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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.
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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.















