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Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons

B. R. MacKenzie*, W. C. Leggett

Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montréal, Québec, Canada H3A 1B1

ABSTRACT: The rate at which turbulent kinetic energy is dissipated influences growth, encounter probability, coagulation rates and vertical distribution of plankton. In this study we quantified the effectiveness with which boundary (wall) layer theory represents turbulent dissipation rates (ε, W m^{-3}) measured within natural surface mixing layers. This model explained 58% of the variance in 818 literature-derived estimates of turbulent dissipation rates measured at 11 different geographic sites. The residual mean square error (RMSE) associated with the regression of $\log_{10}$ observed dissipation rate vs $\log_{10}$ predicted dissipation rate showed that ca 68% of surface layer dissipation rates observed in nature were within a factor ± 5.2-fold of dissipation rates estimated using boundary layer theory. Dissipation rates in more complex mixing environments, where turbulence was known to be caused by additional hydrographic phenomena (free convection, breaking of waves in the upper 1.5 m of the water column, current shear, upwelling), exceeded the boundary layer prediction by 1.5- to 26-fold depending on the mechanism associated with turbulence-generation. We found no evidence that turbulence near the surface (0 to 5 or 0 to 10 m) during high winds (≥ 7.5 or ≥ 10 m s^{-1}) was higher than the boundary layer prediction. When all data were combined into one data set, n = 1088), a multiple regression model having wind speed (W) and sampling depth (z) as inputs ($\log \varepsilon = 2.688 \log W - 1.322 \log z - 4.812$) explained 54% of the variance in surface layer turbulent dissipation rates (RMSE = ± 5.5-fold). The potential for developing more precise empirical models of mixing layer turbulent dissipation rates is high and can be achieved by reporting wind conditions prior to, and during, turbulence measurements more thoroughly, and by collecting replicate turbulence profiles. The existing theoretical and empirical models are, however, adequate for many biological applications such as estimating the nature and magnitude of interactions among, and distributions of, many plankton taxa as a result of wind forcing.

INTRODUCTION

The rate of dissipation of turbulent kinetic energy in aquatic environments has important effects on several aspects of plankton ecology. Turbulence can inhibit growth rates of some phytoplankton species (Belayev 1992, Thomas & Gibson 1992), increase coagulation and sedimentation rates of phytoplankton cells (Kiørboe et al. 1990, Riebesell 1991), enhance encounter rates between zooplankton predators and their prey (Rothschild & Osborn 1988, Marrasé et al. 1990, Sundby & Fossum 1990, MacKenzie & Leggett 1991), and increase development, metabolic and ingestion rates in zooplankton (Saiz & Alcaraz 1991, Saiz et al. 1992).

Turbulent dissipation rates have now been measured in many diverse hydrographic settings (Rothschild & Osborn 1990). In the surface mixing layer, these rates have been compared with predictions made by a simple theoretical model which uses wind velocity and sample depth as inputs (Soloviev et al. 1988). The theoretical model which has been used for these comparisons was derived from the characteristics of constant stress shear flow near a solid boundary (Lumley & Panofsky 1964, Soloviev et al. 1988). This model is considered to be a reasonable first-order description of dissipation rates within the surface layer of the water

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* Present address: Danish Institute for Fisheries and Marine Research, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

column (Dillon et al. 1981, Oakey 1985), particularly when wind is the dominant mechanism responsible for surface layer turbulence.

However, this theoretical model assumes that wind-induced shear is the only turbulence-generating mechanism, even though many other physical processes (e.g. wave-breaking, Langmuir circulations, upwelling) can produce turbulence near the surface (Kitaigorodskii et al. 1983, Oakey 1985, Csanady 1989). In addition, biological phenomena can also increase (Farmer et al. 1987) or decrease (Jenkinson 1986) turbulent dissipation rates. These observations suggest that under some circumstances organisms living within the surface layer will experience turbulence having magnitude and variance greater than that predicted from local wind conditions. This, in turn, might translate into higher levels of variability in biological processes (e.g. encounter rates, coagulation) than would be expected if wind were the only source of turbulence in the surface layer.

Presently, the proportion of total variability in surface layer turbulence that can be attributed to local wind conditions, and to other hydrographic phenomena, is unknown. It is also uncertain whether turbulence in some environments deviates systematically from the boundary-layer prediction, and whether such deviations are sufficiently large to affect biological processes. These statistical aspects of the boundary layer model have potential utility for estimating the ways in which plankton may respond to surface layer turbulence and its variability, and for estimating the importance of different hydrographic processes in producing surface layer turbulence (Kitaigorodskii et al. 1983, Agrawal et al. 1992).

In this paper, we quantify the proportion of the total variance in mixing layer dissipation rates that can be explained by the theoretical (boundary layer) model, and we estimate the magnitude of deviations in the mixing layer dissipation rates from model predictions. We then quantify the deviations in upwelling, convection and wave-breaking dissipation rates from estimates made by boundary layer theory. This theoretical model, if reliable in estimating *in situ* dissipation rates from wind data, could help biological oceanographers understand plankton (Rothschild & Osborn 1988, Riebesell 1991, Kiørboe 1993) and possibly fishery (Cury & Roy 1989, Sundby & Fossum 1990, Ware & Thompson 1991) dynamics when direct measures of dissipation rates are not available.

METHODS

General approach. Our analyses are intended to quantify general relationships between mixing layer turbulent dissipation rates and local wind conditions in environments having little or no tidal energy input. To meet this objective, we extracted estimates of turbulent dissipation rates, wind speeds and sampling depths from the physical oceanographic literature. These data were compared with the predictions made by boundary-layer theory (Eq. 1; see below) to quantify the ability of this theory to represent turbulent dissipation rates when (1) wind-induced shear is the dominant mechanism responsible for generating turbulence, and (2) other hydrographic phenomena also contribute turbulence to the upper layer.

Data collection. We used image analysis software to digitize dissipation rates and sample depths when these data were reported in figures ($n = 1082$); otherwise, values were recorded directly from tables ($n = 6$). Dissipation rates obtained using image analysis methods were accurate, on average, to within 2.75 % of those reported in the original papers. The maximum measurement error, which was associated with 9.5 % of all the observations in our data set was 9.3 %. The average error introduced into our analyses by digitizing turbulence data reported in figures was <10 % of the errors associated with the original instruments used to measure dissipation rates (see Osborn 1978, Lange 1981, Oakey & Elliott 1982).

Mixed layer depths were provided directly in the text or tables of 12 studies surveyed (741 dissipation rate estimates). In 3 other cases (i.e. Osborn 1978, Dillon & Caldwell 1980, Dewey & Moum 1990), we estimated mixed layer depths from temperature or density profiles obtained concurrently with the reported vertical turbulence profiles (347 dissipation rate estimates). The average and maximum errors created by digitizing sample depths were 1.5 and 2.4 m respectively. We excluded all other studies for which the mixed layer depth was not reported or could not be reconstructed for a turbulence profile. In cases where the mixed layer depth exceeded 150 m, we restricted our data collection to depths <150 m, which includes the photic zone in most areas of the sea (Jerlov 1968). In addition, we also excluded dissipation rates measured in and below the thermocline because stratification inhibits mixing (Denman & Gargett 1983, p. 804; also Fig. 1 in Yamazaki 1990).

Most studies which we surveyed (14 of 15) provided daily-averaged wind speeds for those days when turbulence profiles were obtained. In one study (Lueck et al. 1983) from which we extracted 6 dissipation rate estimates, wind speed was reported only as a range for the entire sampling period. We chose the range midpoint to represent the approximate wind speed which prevailed when dissipation rates were being measured in this study. All measures of wind speed, including those based on the Beaufort wind scale ($n = 176$; Osborn 1978), were converted to m s^{-1}.

Data analyses. The boundary layer model (e.g. Oakey 1985, Agrawal et al. 1992) states that dissipation rates (ε, W m^{-3}) adjacent to a solid boundary will scale with energy input (e.g wind) and distance from the boundary (e.g. depth):

$$\begin{aligned}\varepsilon &= [(\rho_a/\rho_w)C_D]^{3/2} \times [W^3/(0.4\,z)] \\ &\quad \times (1\ \mathrm{W\ m^{-3}}/0.001\ \mathrm{m^2\ s^{-3}}) \\ &= (5.82 \times 10^{-6})\ W^3/z \end{aligned} \tag{1}$$

where W = wind speed (m s^{-1}); z = sampling depth (m); ρ_a = density of air (1.2 kg m^{-3}; Loder & Greenberg 1986); ρ_w = density of seawater (1025 kg m^{-3}; Lueck 1988); C_D = coefficient of drag between the water surface and the wind (0.0015; Loder & Greenberg 1986); and 0.4 = von Karmann's constant (Lumley & Panofsky 1964).

Dissipation rates estimated with this model can, therefore, be compared with those measured in the mixed layer. For this comparison, we first restricted our analyses to dissipation rates (n = 818) collected in regions where wind energy was the dominant source of turbulent kinetic energy (see Table 1 for data sources).

We calculated R^2, the proportion of variation in the observed dissipation rates that was explained by Eq. 1, for dissipation rates extracted from these studies. The magnitude of R^2 indicates the proportion of total variance in the observed dissipation rates associated with wind speed and sampling depth, relative to the variance associated with other variables not included in Eq. 1 but known to influence dissipation rates (e.g. wave height, intersite differences in mixing layer salinities). We next calculated the slope and intercept of the regression line relating the observed and predicted dissipation rates to explore systematic deviations of the model from observations. Eq. 1 will be shown to systematically underestimate (or overestimate) observed turbulent dissipation rates contained in our data set if these regression coefficients differ significantly from 1 and 0 respectively. We next used the residual mean square error (RMSE) associated with the regression line relating observed and theoretically-predicted dissipation rates to estimate the standard deviation of observed values from those predicted by Eq. 1.

We also considered dissipation rates (n = 270) that were measured in environments known to have mechanisms in addition to wind that generate turbulence in the surface layer. These studies, and the environments in which the dissipation rates were measured, are described by Dewey & Moum 1990 (upwelling meander), Kitaigorodskii et al. 1983 (wave-breaking region near water surface), Oakey & Elliott 1982 (water column shear due to currents; see also Oakey 1985), and Shay & Gregg 1986 (convectively-driven turbulence). For each of these studies, we calculated the average value of the difference between the observed and theoretically-predicted (Eq. 1) dissipation rate. These values estimate the amount by which turbulence in each environment deviated from dissipation rates expected from local wind mixing alone.

Finally, we combined all reported dissipation rates into one data set. This data set was then used to develop a general empirical model of mixing layer turbulent dissipation rates for use in situations where hydrographic conditions (e.g. multiple sources of turbulence) prevent application of Eq. 1, and where instrumentation for directly measuring dissipation rates is unavailable.

RESULTS

Data set

We extracted data from 15 studies which were conducted in 14 different geographic regions (Table 1). The data are summarized statistically in Table 2. Thirteen study sites were situated in marine environments (1076 dissipation rate estimates) and 2 were in lakes or reservoirs (12 dissipation rate estimates). Seventy-five percent of the observations used in our analyses were recorded within the upper 44 m of the water column, and the remainder were recorded at depths between 44 and 150 m.

Data analyses

Environments having wind as the dominant source of turbulence

The boundary-layer model (Eq. 1) explained 58 % ($p < 0.0001$) of the variance in dissipation rates measured within the surface mixing layer (Table 3, Model 1). The intercept of the regression line for the scatterplot of observed vs predicted dissipation rates did not differ significantly from 0 ($p > 0.05$), but the slope (1.100) was significantly greater than 1 (*t*-test: $p < 0.005$; Zar 1984). Eq. 1 therefore overestimated the dissipation rates contained in our data set. The overestimation was, however, small. The RMSE associated with the observed vs predicted scatterplot was 0.715. This indicates that ca 68 % of the dissipation rates in our data set were within a factor of $\pm$ 5.2 (= $10^{0.715}$) of the values predicted by Eq. 1.

When the influences of wind speed and sampling depth were considered separately in linear regression models, the regression coefficients for the wind and depth inputs were 2.698 and –1.216 (Table 3, Models 2 and 3). Wind speed and sampling depth explained 26

Table 1. Data sources, geographic locations of sampling sites, and the number of observations extracted from studies which provided turbulent dissipation rates. Those studies conducted in areas where wind stress was the principal source of turbulence are indicated as 'Wind', and those studies conducted in areas where additional important sources of turbulence were present are indicated as 'Other'

	Source	Region	n	Source of turbulence
1	Dewey & Moum 1990 (Fig. 7a.i, a.v, b.i, b.v, c.i, c.v)	Central coast of California, USA (outside upwelling meander)	55	Wind
2	Dewey & Moum 1990 (Fig. 7a.ii, a.iii, a.iv, b.ii, b.iii, b.iv, c.ii, c.iii, c.iv)	Central coast of California, USA (inside upwelling meander)	67	Other
3	Dillon & Caldwell 1980 (Figs. 8 & 9)	Stn P (50° N, 145° W)	49	Wind
4	Dillon et al. 1981 (Fig. 2)	Green Peter Reservoir	6	Wind
5	Haury et al. 1990 (Fig. 5)	Monterey Bay, USA	103	Wind
6	Kitaigorodskii et al. 1983 (Table 5)	Lake Ontario	6	Other
7	Lange 1981 (Fig. 6)	Stn P (50° N, 145° W)	112	Wind
8	Lueck 1988 (Figs. 4, 5, 6, 10, 11, 12, 14 & 16)	30° N, 154° W	173	Wind
9	Lueck et al. 1983 (Figs. 4 & 7)	49° N, 127° W	6	Wind
10	Moum & Caldwell 1985 (Fig. 2)	0° N, 140° W	24	Wind
11	Oakey 1985 (Fig. 4)	59° N, 12° W	27	Wind
12	Oakey & Elliott 1982 (Fig. 16)	Emerald Basin, Scotian Shelf	30	Other
13	Osborn 1978 (Figs. 2, 3, 4, 6, 7, 8, 9, 10, 11, 12)	5-80 km west of Santa Maria, Azores	176	Wind
14	Shay & Gregg 1986 (Fig. 15; averaged profile)	Convective averaged turbulence near Bahamas	82	Other
15	Shay & Gregg 1986 (Fig. 16; averaged profile)	Convective turbulence in warm-core ring near Bermuda	85	Other
16	Soloviev et al. 1988 (Fig. 7)	39° N, 20° W	46	Wind
17	Veth 1983 (Fig. 12)	54° 30′ N, 4° 30′ E	41	Wind

and 30 %, respectively, of the variability in these dissipation rates. A multiple regression model employing wind speed and sampling depth as inputs explained essentially the same proportion of the total variance ($R^2 = 0.60$) as Eq. 1 ($R^2 = 0.58$).

Environments having multiple sources of turbulence

Four studies reported dissipation rates within the wind-mixed surface layer on occasions when other hydrographic processes were known to be important contributors to the overall level of turbulence in the water column (Table 1). These data were gathered in an upwelling meander, the near-surface wave-breaking region of the water column, a continental shelf environment having current shear due to water mass movement, and in 2 free-convectively mixing water columns. The ranges of wind speeds and sampling depths for these studies were 1.6 to 11.7 m s^{-1} and 0 to 150 m, and generally overlapped the ranges of wind speed and sampling depth observed in the previous section ('Environments having wind ...').

Dissipation rates deviated maximally from the wall-layer prediction in the near-surface region of the water column (0 to 1 m). These dissipation rates exceeded the levels of turbulence expected from wind-induced shear by an average of 26-fold (Fig. 1A). Since these higher rates of dissipation were probably associated with wave-breaking during high winds (see Kitaigorodskii et al. 1983), we attempted to determine whether such deviations were also present in the data set used to evaluate Eq. 1 (see 'Environments having wind ...').

We evaluated this hypothesis by extracting from the hypothesized 'wind-only' data set those dissipation rates which were measured at shallow depths and during high winds. We, therefore, retained dissipation rates measured only when wind speed was ≥ 7.5 m s^{-1} (since higher wind speeds produce wavebreaking; Pond & Pickard 1983), and which were recorded at sampling depths ≤ 10 m. This combination of wind speed and sampling depth may therefore show evi-

Table 2. Summary of wind speeds, sampling depths and turbulent dissipation rates used in statistical analyses. See Table 1 for author codes corresponding to data sources

Data sources	Variable	n	Mean	SD	Median	Minimum	Maximum
1, 3, 4, 5, 7–11, 13, 16 & 17	Wind	818	7.4	3.5	5.8	1.9	15.5
	Depth	818	34.6	32.7	20.4	0.2	150.0
	Log ε	818	–4.574	1.107	–4.638	–7.542	–1.930
2, 6, 12, 14 & 15	Wind	270	6.3	2.3	5.5	1.6	11.7
	Depth	270	28.6	18.3	23.3	0.4	78.6
	Log ε	270	–3.905	0.895	–3.963	–5.599	–0.319
1–17	Wind	1088	7.1	3.3	5.8	1.9	15.5
	Depth	1088	33.1	29.9	20.8	0.2	150.0
	Log ε	1088	–4.408	1.097	–4.362	–7.542	–0.319

dence of enhanced energy dissipation compared to the boundary layer prediction. However, these dissipation rates, derived from 8 different studies, were on average only 38 % of the values estimated by the wall-layer model (n = 36; Fig. 1A, Table 4). Similar analyses using dissipation rates measured for other combinations of wind speed and sampling depths showed no evidence of enhanced dissipation that may have been associated with wave-breaking (Table 4).

Convectively-driven turbulence (Shay & Gregg 1986) measured inside a Gulf Stream warm-core ring exceeded wind-induced turbulence by an average of 3.7-fold (Fig. 1B), although some individual measurements exceeded the boundary layer prediction by 10- to 30-fold. Another convectively mixing water column located outside the warm core ring had turbulent dissipation rates which exceeded the boundary layer prediction by 1.3-fold (Fig. 1B). Dissipation rates measured on a continental shelf in the presence of near-inertial current shear (Oakey & Elliott 1982; see Oakey 1985, p. 1668) were 3.5-fold higher than turbulence levels expected from local wind conditions (Fig. 1C). Dissipation rates measured within an upwelling meander near the coast of California exceeded the boundary layer prediction by 1.8-fold (Fig. 1D).

The higher levels of turbulence in 3 of these more complex environments (i.e. continental shelf with inertial current shear, convection inside and outside a warm core ring, a California current upwelling meander) were within the range of error associated with the relationship between the observed dissipation rates within a wind-induced mixing layer and those predicted by Eq. 1 (RMSE = 0.715; see Table 3, Model 1). This observation suggests that wind-based models may be powerful general indicators of the level of upper layer turbulence even in complex hydrographic situations where multiple sources of turbulence exist.

When all of the data were combined into one data set (n = 1088), Eq. 1 explained 52 % of the variability in these estimates (Table 3, Model 5). The slope and intercept of the observed vs predicted scatterplot did not differ significantly from 1 and 0 respectively ($p > 0.05$). By comparison, a multiple regression model having wind speed and sampling depth as inputs explained 54 % of the variability in these dissipation rates (Table 3, Model 6). The difference in correlation coefficients is not statistically significant ($p > 0.05$).

Table 3. Theoretical and empirical models of the dependance of upper layer turbulent dissipation rates on wind speed and sampling depth in areas where tidal energy inputs were negligible. Note that Models 1 and 5 correspond to the prediction derived from boundary layer theory (see Eq. 1 in text). Parameters of regression models are accompanied by standard errors. RMSE: residual mean square error; SSE: total sum of squares of deviations from ε; and $\bar{y}$: mean of log ε (W m^{-3}) in the data set. p-values for statistical significance of models and input variables are all < 0.0001. Logarithmic transformations are base 10. Data sources for Models 1 to 4 (n = 818) are authors 1, 3, 4, 5, 7, 8, 9, 10, 11, 13, 16 and 17 (see Table 1). All studies listed in Table 1 provided data for Models 5 and 6 (n = 1088)

Model	R^2	n	RMSE	SSE	$\bar{y}$
1 $\log \varepsilon = \log(5.82 \times 10^{-6} \times W^3/z)$	0.58	818	0.715	416.7	–4.574
2 $\log \varepsilon = (2.698 \pm 0.160) \log W - (6.782 \pm 0.135)$	0.26	818	0.955	743.7	–4.574
3 $\log \varepsilon = (-1.216 \pm 0.065) \log z - (2.958 \pm 0.093)$	0.29	818	0.929	704.2	–4.574
4 $\log \varepsilon = (2.926 \pm 0.118) \log W - (1.306 \pm 0.050) \log z - (5.232 \pm 0.116)$	0.60	818	0.702	402.2	–4.574
5 $\log \varepsilon = \log(5.82 \times 10^{-6} \times W^3/z)$	0.52	1088	0.760	626.9	–4.408
6 $\log \varepsilon = (2.688 \pm 0.110) \log W - (1.322 \pm 0.048) \log z - (4.812 \pm 0.109)$	0.54	1088	0.742	598.0	–4.408

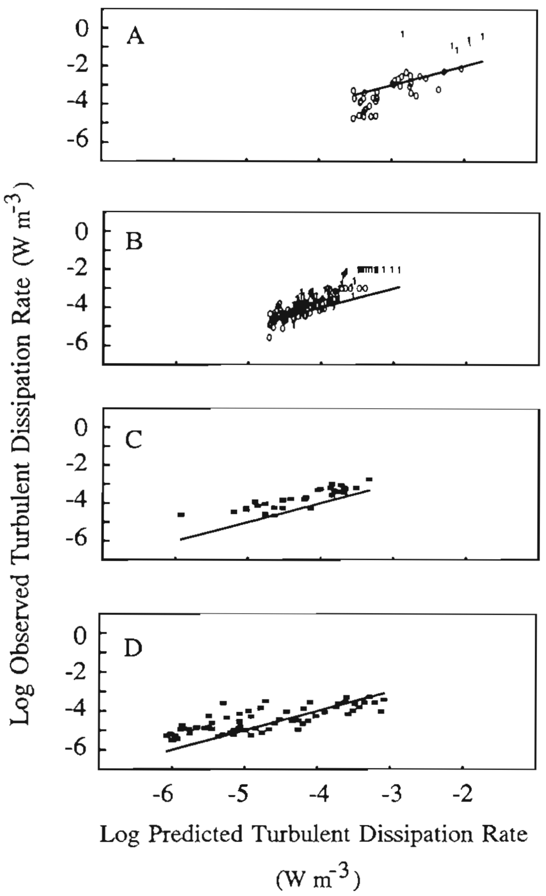

Fig. 1. Turbulent dissipation rates in environments known to have multiple sources of turbulent kinetic energy. All scatterplots show log observed dissipation rate vs log predicted dissipation rate, where the predicted values were calculated using Eq. 1 Diagonal lines on each panel are the 1:1 reference lines. (A) Symbol code '1' represents near-surface turbulence associated with wave-breaking (n = 6; Kitaigorodskii et al. 1983). The remaining symbols ('0') represent turbulent dissipation rates measured in other environments at depths 0 to 10 m during wind speeds ≥7.5 m s^{-1} (data sources were authors 1, 5, 7, 8 & 17, see Table 1; n = 36). (B) Turbulence associated with free-convectively mixing water columns (Shay & Gregg 1986). '0' denotes dissipation rates measured on the continental shelf near the Bahamas (n = 82) and '1' denotes dissipation rates measured in a Gulf Stream warm core ring (n = 85). (C) Turbulence on a continental shelf in the presence of near-inertial current shear (Oakey & Elliott 1982; n = 30). (D) Turbulence inside an upwelling meander near the California coast (Dewey & Moum 1990; n = 67)

DISCUSSION

Critically evaluating the power and reliability of existing models (e.g. Rice & Cochran 1984, Hall 1988), and developing new models are important initial steps in estimating how natural phenomena or populations might vary at other times or places (Peters & Downing 1984, Rice & Cochran 1984, Hall 1988, GLOBEC 1991).

Table 4. Turbulent dissipation rates measured near the sea surface (0 to 10 m) during wind conditions (>7.5 m s^{-1}) likely to produce wave-breaking. Residual is the amount by which the mean of log ε differed from the value of log ε predicted by Eq. 1 See Table 1 for author codes corresponding to data sources

W (m s^{-1})	z (m)	Residual	n	Data sources
≥7.5	≤ 5	−1.566	6	5, 8
≥10.0	≤ 5	−0.220	5	5, 8
≥7.5	≤10	−0.416	36	1, 5, 7, 8 & 17
≥10.0	≤10	−0.147	19	1, 5, 8 & 17

The analyses we report here represent the first statistical evaluations of the influence of wind speed and sampling depth on variability in turbulent dissipation rates within the surface mixing layer. They also provide the first direct quantitative comparison of the effectiveness of the most frequently referenced theoretical model for representing the depth-dependent rate of dissipation of wind generated turbulent kinetic energy in aquatic systems.

The principle findings of our analyses are: (1) simple theoretical and empirical models can explain up to 60% of the variance in these rates; (2) the standard deviation of dissipation rates predicted by boundary-layer theory, or wind-based multiple regression models, is approximately a 5-fold multiple of the value predicted by these models; and (3) wind speed and sample depth contribute essentially equally to the explained variance in the dissipation rates in our data set. We note that the constant stress shear flow model (Eq. 1) is virtually identical to another model (Simpson & Bowers 1981) of turbulent energy dissipation within the surface layer. The Simpson & Bowers model also assumes that, in areas of negligible tidal activity, energy dissipation $\propto W^3/z$. It is likely, therefore, that the Simpson & Bowers model will be equally effective in explaining variability in mixing layer dissipation as the models considered here (Table 3).

These analyses emphasize the highly significant, and dominant, influence of wind speed on surface layer turbulence levels (Kullenberg 1976, Lueck & Reid 1984). Dissipation rates measured across geographic regions and hydrographic settings, and derived using diverse instrumentation and sampling methods, conformed broadly to the theoretical nature of boundary-layer mixing (Table 3). This finding suggests that wind speed is one of the most important environmental variables to be measured and reported during studies of turbulence and/or plankton biology. This result also implies that it may be difficult to identify or rank the influence of other hydrographic or biological factors on surface layer turbulence unless the effect of wind speed is first statistically removed.

This can be achieved by using one of the models evaluated or developed here (Table 3). In doing so, for example, we have found that convection in a warm core ring during boreal winter contributed on average nearly 4-fold more turbulence than that expected from local wind conditions, and that the contribution of convection to turbulence can sometimes be substantially higher (Fig. 1B).

The 95 % confidence limits for a single estimate of turbulent dissipation rate are very large (>± 10 times the mean; Table 3), even when hydrographic conditions appear to be relatively simple (i.e. a surface wind-mixing layer). This is likely to be a consequence of at least 2 factors. First, there were almost certainly additional phenomena that increased or decreased dissipation rates above or below those estimated with wind-based descriptions of mixing layer turbulence. These phenomena would include Langmuir circulations, current shears that are unrelated to wind conditions but which interact with bathymetry (Wolankski & Hamner 1988), and possibly biological factors. [For example swimming fish can increase local dissipation rates by 10-fold compared to background levels (Farmer et al. 1987), and phytoplankton exudates, which can increase seawater viscosity, can suppress turbulent dissipation rates (Jenkinson 1986).]

Second, sampling methods and data reporting procedures are also likely to contribute significantly to the residual variability associated with the models we have considered. For example, the measures of wind energy input to the water column used in our analyses assume that steady state wind conditions prevailed prior to, and during, the measurement of turbulent dissipation rates. This assumption was necessary because (1) the appropriate time lag between changes in wind speed and subsequent changes in dissipation rate has not been studied systematically *in situ*, although turbulent dissipation rates have been observed to increase within an hour of an increase in wind speed (Dewey & Moum 1990, see also Dillon & Caldwell 1980), and (2) most studies which provided data for our analyses did not present a time series of wind conditions. Consequently, some of the dissipation rate estimates in our data set may not adequately reflect high-frequency fluctuations in wind conditions that may have occurred shortly before some turbulence profiles were obtained. As a direct consequence, the influence of wind speed on surface layer mixing that we report (Table 3) should be viewed as a minimum estimate of its true effect on dissipation rate variability.

Moreover, many of the studies from which we derived data for our analyses contained unreplicated turbulence profiles. Turbulence is however recognized to be an extremely variable, intermittent process (Lazier & Mann 1989, Gibson 1990). Replicate profiles obtained within minutes of one another can differ by an order of magnitude (Osborn 1978, Oakey 1985). Consequently, individual turbulence profiles may not be truly indicative of the dominant mechanism (e.g. wind) responsible for turbulence in a particular environment (Gibson 1990). It has been shown that, if individual profiles are averaged, the mean profile obtained is more closely related to wind conditions than are the individual profiles (e.g. Dillon & Caldwell 1980, p. 1915; Oakey 1985, p. 1671; Shay & Gregg 1986, p. 1789; Gibson 1990). Development of new empirical models based on replicated profiles should significantly reduce the residual variation associated with such models considerably.

We note that during our search for dissipation rate estimates, we found many published reports which failed to provide any measure of wind speeds during or adjacent to the times when dissipation rates were measured. Consequently, we could not include these rates in our data set. However, the fact that no other single process has yet been shown to explain an equivalent proportion of total variance ($R^2 = 0.26$) in *in situ* dissipation rates within the surface layer across sites and depths, indicates that future studies of turbulent dissipation should routinely include measurements of wind speed prior to and during the sampling interval. This minor improvement in data reporting would facilitate comparisons of turbulence measurements across environments (e.g. Fig. 1) and of *in situ* dissipation rates with estimates derived from theoretical and empirical models (e.g. Table 3).

Turbulent dissipation rates in the upper 1 to 1.5 m are much higher than those predicted by boundary layer theory (Kitaigorodskii et al. 1983, Agawal et al. 1992). However, exceptionally high dissipation rates during high winds do not appear to extend to greater depths (Fig. 1A, Table 4). Our analyses showed that when wind speeds were sufficient to cause wave-breaking (wind speeds >7.5 m s^{-1}), dissipation rates near the surface (upper 5 to 10 m) did not exceed the boundary layer prediction by large amounts. This suggests that the depth range of enhanced dissipation (relative to the boundary layer prediction) associated with surface wave breaking may be very shallow.

Our exploratory analyses of the influence of wave-breaking on near-surface dissipation rates were, however, based on a relatively small number of dissipation rate estimates (Table 4). In addition, some of these estimates may not have been measured under fully developed sea conditions (i.e. when significant wave height has attained its maximum value for a particular combination of wind speed, duration and fetch). In the case of a 10 m s^{-1} wind, full sea state would only occur after the wind had been blowing for at least 10 h across a fetch exceeding 130 km (Pond & Pickard 1983). Only under fully developed sea conditions would the contribution of wave breaking to mixing layer turbulence be maximal. We cannot exclude, therefore, the possibility that a study employing appropriate instrumentation and sampling methods during a fully developed sea state might be able to detect dissipation rates which exceed the boundary layer prediction at depths >1.5 m.

Biological implications

Variability in the dissipation rate of turbulent energy within aquatic ecosystems is an important component of the environmental heterogeneity experienced by planktonic organisms. Consequently, turbulent dissipation is likely to have a pervasive influence on several aspects of plankton ecology. From an evolutionary perspective, the upper layer of stratified seas, and of lakes, represents a habitat that has predictably high rates of dissipation of kinetic energy relative to deeper layers (Table 3), and the magnitude of these rates can vary in predictable ways. For example, mixing layer dissipation rates can vary daily (Moum & Caldwell 1985), seasonally and annually (Rothschild & Osborn 1988) because of frequency-dependent variablility in wind speed (Taggart & Leggett 1987, Colin & Garzoli 1988) or heat input/loss (Moum & Caldwell 1985). Clearly, planktonic taxa, and benthic and nektonic taxa with planktonic life stages, have had ample time to adapt their behavioural and lifehistory characteristics to these predictable characteristics of mixed layer dissipation (e.g. Margalef 1978).

Turbulence also has an important role in determining the size of phytoplankton cells in different hydrodynamic environments (Margalef 1978), and the rate at which these cells coagulate and settle from the water column (Kiørboe et al. 1990, Riebesell 1991). Pelagic food web structure (Kiørboe 1993), rates of secondary production by copepods (Dam & Peterson 1991), and the proportion of primary production which is consumed by higher trophic levels (including fish populations; Legendre 1990, Kiørboe 1993), may all depend on phytoplankton cell size, which, in turn, is believed to be hydrodynamically controlled (Margalef 1978, Cushing 1989, Legendre 1990). These recent findings suggest that interannual variability in pelagic food web structure ('classical' vs 'microbial'; Kiørboe 1993) and in the rates of production at higher trophic levels in stratified seas, and lakes, may be partly determined by levels of turbulence induced by wind energy inputs, which as we have shown, can be estimated using simple models (Table 3).

In this connection, we note that, in general, the models evaluated here (Table 3), and their 95% confidence limits, can provide realistic bounds for *in situ* ranges of turbulent dissipation rate, and for parameters derived from these dissipation rates (e.g. encounter rates: MacKenzie & Leggett 1991; phytoplankton coagulation rates: Kiørboe et al. 1990). We have shown, using an earlier version of Model 6 (MacKenzie & Leggett 1991), that the confidence limits about some of these derived parameters may be substantially less than those associated with $\hat{\varepsilon}$ itself, if $\hat{\varepsilon}$ is subsequently used in nonlinear models whose terms have exponents <1.

This suggests that only major and persistent sources of turbulence (e.g. tides, strong upwelling) will produce sufficiently large deviations from boundary layer theory to have a systematic and sustained impact on, for example, encounter rates that would not be anticipated on the basis of wind-mixing alone. We suspect, therefore, that those biological responses that are sensitive to turbulence will generally reflect dissipation rates averaged over time scales which exceed those associated with turbulent velocity fluctuations (seconds to tens of seconds: Oakey & Elliott 1982). [For example, Lewis et al. (1984) found that the photosynthetic rate per unit chlorophyll of phytoplankton cells freely circulating within the mixing layer of Bedford Basin (Nova Scotia, Canada) was highly correlated to the mean of 6 to 7 depth-averaged turbulent dissipation rates obtained within a time span of 25 min.] The findings of Lewis et al. (1984) demonstrate that brief (seconds to tens of seconds) and/or infrequent events of high (or low) turbulence, which are likely to have contributed to the unexplained variance in our statistical analyses, are unlikely to have an appreciable effect on those turbulence-sensitive biological rates which require exposure to longer periods (e.g. >1 h) of high (or low) turbulence before they adapt to new values.

For many practical biological applications, therefore, the simple wind-based models evaluated and developed here may provide reasonable measures of surface layer turbulence relevant to living organisms. Turbulence estimates derived from these models may explain significant portions of the variability in these processes, even though (1) the natural physical environment may be hydrographically complex and (2) turbulent dissipation is an intermittent process at short time and space scales (Lazier & Mann 1989, Nelkin 1992).

We conclude that the dissipation rate models considered here can be effectively employed to consider the potential influences of turbulence on biological processes when instrumentation required for direct estimation of ε is unavailable. We expect, and hope, that improved models will soon be developed, given the increasing recognition of the importance of small-scale turbulence to plankton ecology. Given the assumptions required in our analyses, the potential for such improvement, with only minimal modification to existing sampling and reporting protocols, appears to be great. Towards this end, we recommend that investigators measure and report ε and other relevant environmental variables (e.g. wind speed, stratification, wave state, etc.) routinely and effectively in the future.

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