EFFECT OF TURBULENT MIXING ON THE MARINE PLANKTON VERTICAL DISTRIBUTION: MODEL SIMULATIONS

ABSTRACT: The effect of the turbulent mixing processes within fine structure of hydrophysical field on the prey and predator biomass is presented. The calculations were made on the basis of an one-dimensional prey-predator ecosystem model on the assumption of an absolutely stable vertical distribution of the average sea water density and that vertically intermittent layer are horizontally homogeneous. This model was tested with data obtained from the southern Gdansk Gulf (Baltic Sea). The vertical distributions of temperature and salinity fields were taken as initial conditions for various simulations. The numerical simulations were computed for different values of the wind speed. This study reveals that an intensity of the layer-mixing increase with the increase of the wind speed and duration of the turbulent disturbance. For low values of wind speed \(U_{10} < 2 \text{ m s}^{-1}\) and for short time of action of hydrodynamic sources of mixing \(t_i < 60 \text{ min.}\), fine-scale interlayering is not created in investigated case. It is also shown that the thicker the layer, the smaller the structural anomaly. The presented results demonstrate that the dynamic processes are responsible for the shape of vertical profiles of investigated characteristics to the same extent as physiological processes. Hydrodynamic conditions play a basic role where the microstructure of investigated functions is concerned.

KEY WORDS: Marine plankton, Turbulent mixing, Fine-scale, Prey, Predator

1. INTRODUCTION

Since the mid-1970s oceanographers and marine physicists have performed the investigations in laboratory and in situ of fine-scale variations in the structure of the hydrophysical fields of the ocean, both in time and in space. Following the implementation of increasingly accurate sensors and recording instruments to measure the thermal, salinity and dynamic states of the sea, it soon became clear that its hydrophysical fields are intermittently stratified in the vertical. Water layers displaying horizontal uniformity of flow velocity, temperature, salinity, density over a distance of several kilometres are by contrast homogeneous in the vertical over much shorter distances (Druet et al. 2003).

How long such intermittent stratification remains is not well known. The only assumption one can make is that this period is at least 10 minutes longer than the time interval separating two successive soundings. One should also recall that some of these structures can last up to a month, for example, in the tropical north-west Atlan-
tic, or even a year, when the inhomogeneity has been created by a large-scale thermohaline circulation. The geometrical structure of these intermittent stratifications is such that vertically uniform or quasi-uniform layers c. 0.5–15 m thick are interspersed by much thinner layers (c. 5–50 cm thick) with characteristically steep vertical gradients of the water’s physical properties. This kind of vertical stratification has become known as “fine structure” or “small-scale stratification” (Monin and Ozmidov 1981, Ozmidov 1983). The continuous vertical distribution of the physical properties of the water \( u = T, S, \rho, u \), recorded by a sufficiently sensitive meter at instant \( t_0 \), can be divided into three component profiles:

\[
\mathbf{v}(x, y, z, t_0) = \mathbf{v}(z, t_0) + \mathbf{v}'(x, y, z, t_0)
\]

where the \((-)z\) axis points downwards in accordance with the direction of action of the gravitational force. The \( \mathbf{v}(z) \) profile reflects the classic, smooth vertical distribution of values averaged over a longer period of time, and is comparable with profiles obtained by means of point measurements. In the case of temperature, the measurement will have been performed with a reversible thermometer, and the salinity will have been determined by chemical analysis of water samples. The \( \mathbf{v}'(x, y, z, t_0) \) profile reflects the changes generated by micro-scale turbulence in the flow velocity field of the water masses, while the \( \tilde{\mathbf{v}}(z, t_0) \) profile represents the fine structure.

The fine structure is shaped by the gravitational and inertial instability of the water masses and water flow, which generates turbulent mixing at depths where the laminar flow of the water, described by the Kelvin-Helmholtz equation, has been disturbed (inertial instability), or where there has been horizontal, intrusional interlayering of water masses differing from the surroundings in temperature and salinity (gravitational instability). In the latter case, mixing is caused either by thermal convection or by the formation of “salt fingers”. Medium- and large-scale gravitational instability leading to abyssal subsidence of water does not give rise to fine-scale vertical stratification.

Regardless of how these mixing processes are initiated, the dynamic characteristics of the fine structure are qualitatively almost identical in all three types of vertical stratification. That is to say, the homogeneous layers are more or less well mixed layers, while the flow of water in the intervening thin, steeply-gradiented layers is, as a rule, laminar or quasi-laminar. If such an intermittent stratification of water masses endures for 15 minutes and more, it can be classified as fine structure.

The study of the influence, exerted by turbulent mixing processes in the intermittent fine structure on the behavioural states of marine plankton was shown by Druet and ZIELIŃSKI (1994). They show clearly the relationship between the concentration of suspended matter and the intensity of turbulent mixing: the more intense the turbulent mixing, the more widely dispersed the cloud of suspended matter and the lower its concentration. The upshot of this is obvious, and the highest concentration of phytoplankton can be expected above or below thin laminar or quasi-laminar interlayers with steep density gradients. Investigations of greater precision usually involve mathematical modelling based on the equation of turbulent diffusion of phytoplankton and the nutrient supply to it. The results of computer simulation studies have shown that the coefficient \( K \) representing turbulent mixing in the diffusion equations exerts a considerable influence on the state of phytoplankton concentration. Homogeneous layers are strongly dispersed with consequent thinning out of the suspended matter, which moves above the laminar gradiental interlayers, where it increases its concentration. One is entitled to pose the question, whether a phytoplankton concentration fine structure does indeed come into existence under natural conditions. The answer can be found either through \textit{in situ} studies, or by performing simulations based on real vertical distributions of the water’s hydrophysical properties.

There is a conviction among oceanographers that this structure must necessarily affect the concentrations of diverse types of suspended matter, in particular the concentration fields of marine phyto- and zooplankton. The intensive, world-wide research effort of the 1980s and 1990s provided incontrovertible evidence that the individual growth of organisms – from larval fish to
herbivorous copepods – is linearly dependent on the food concentration, which varies on a time-scale characterizing the existence of fine structure (Davis et al. 1991). It was also demonstrated that the random movements of predators are negatively correlated with food concentration, so that they tend to stay longer in areas of higher concentrations, i.e. areas where their individual movements can be reduced to a minimum. In short, we can no longer investigate the environmental conditions governing the behaviour of plankton without taking account of the fact that their life processes are affected to a considerable extent by the turbulent mixing that homogenizes the uniform fine structure layers (Druet 2003). The effect of turbulence on predator-prey interactions in plankton has received a great deal of attention in recent years and was examined by Rothschild and Osborn (1988), Evans (1989), Sundby and Fossum (1990), Davis et al. (1991), Granata and Dickey (1991), Yamazaki et al. (1991), MacKenzie and Leggett (1991), Kiørboe (1993), MacKenzie et al. (1994), Sundby et al. (1994), Kiørboe and MacKenzie (1995), Kiørboe and Saize (1995), Caparroy and Carlotti (1996), Lough and Mountain (1996), Dower et al. (1997), Seuront et al. (2001), Dzierzbicka-Głowacka (2006).

The objective of this paper is to present results of an one-dimensional prey-predator ecosystem model (hypothetical model), which show how the turbulent mixing processes, within fine structure of hydrophysical field, will enhance or reduce values of vertical distributions of prey and predator biomass. During the entire numerical experiment *Mysis mixta* – predator “feeds on” *Pseudocalanus minutus elongatus* – prey. The problem described in this paper has not been established earlier and this is a key statement, since it is the motivation and justification for the present study.

The *Pseudocalanus minutus elongatus – Mysis mixta* interactions in the Gulf of Gdansk may not be the most appropriate combination for the study of prey – predator encounters because of not adequate information on behaviour of *M. mixta*. The literature on behaviour of mysids is not very extensive and mainly from fresh waters. In the Baltic Sea the majority of studies have been focused on the musid species inhabiting the open sea areas. Shallow and eutrophicated bays are often characterised by much higher densities of musids than similar open sea areas (Kotta and Kotta, 2001).

Vertical migration and prey selection of the pelagic mysid shrimp, *Mysis mixta*, were studied experimentally in the northern Baltic Sea (the Gulf of Finland, Gulf of Riga (Kotta and Kotta, 2001; Viherluoto and Viitasalo, 2001). The results show that mysid predation is considered to be an important factor affecting zooplankton communities (i.e. mainly Rotifera, *Acartia* spp., *Eurytemora affinis*, *Temora longicornis* and also *Pseudocalanus elongatus*) (Viherluoto and Viitasalo, 2001).

2. VERTICAL DISTRIBUTION OF THE MARINE PLANKTON

The application of turbulent diffusion equations to the modelling of concentrations of herbivorous zooplankton, which in turn are fed upon by larval fish and carnivorous Copepoda, is a task more complex than the modelling of the hydrodynamically passive phytoplankton. Considering the minute sizes of this zooplankton, we can assume, without committing too serious error, that turbulent mixing affects ambush-type microzooplankton in the same way as phytoplankton. However, when modelling zooplankton with a cruise-type behaviour, this assumption has to be rejected, because this zooplankton is capable of active movement. Its relations with a predator hunting for zooplanktonic prey are more complex and the foraging process as a component of the source function cannot be defined in the same way as that of phytoplankton, because the principal factor governing it is the encounter rate between predator and prey (Davis et al. 1991; Druet 2003).

A simple 1D-upper layer model which examine the relative importance of turbulence to change in the vertical distributions of marine plankton (prey and predator) is here presented. Fundamental to the present modelling study is the assumption of an absolutely stable vertical distribution of the average sea water density. This means that the mean
density and salinity of the water increase and the mean temperature falls with depth. Therefore, the hydrodynamic state of mass transfer and exchange in the various intervals of a stably stratified density distribution can be defined by the vertical distribution of the square of the Väisälä-Brunt frequency. If we assume the dynamics of the horizontally quasi-homogeneous upper layer of the ocean in terms of ocean boundary layer dynamics (all horizontal gradients vanish), the equation of the diffusion type for prey biomass, $Z_p$, for weights, $W_p$, and numbers, $Z_p/\rho$, of a herbivorous copepod, can be simplified to the following form (Dzierzbicka-Głowacka 2000; 2006):

$$\frac{\partial W_p}{\partial t} = \text{ING} - \text{FEC} - \text{MET} \tag{1}$$

$$\frac{\partial Z_p}{\partial t} = \frac{\partial}{\partial z} \left( K_z \frac{\partial Z_p}{\partial z} \right) + \text{MIG} - \text{PRED}_p \tag{2}$$

$$Z = \sum W_p Z_p \tag{3}$$

Equation (1) determines the change in weight as the sum (GROWTH = ING – FEC - MET) of gains (ingestion, ING) and losses (zooplankton fecal pellets, FEC, and metabolism, MET) of energy. Equation (2) represents the effects of turbulent diffusion, $K_z$, diurnal migration, MIG, and predation, PRED$_p$, on prey concentration, assuming that all death is due to predation. The processes having the influence on the source/sink function (i.e. ING, FEC, and MET) are given in Appendix I and the detailed description is presented by Dzierzbicka-Głowacka (2000; 2005). The migration process can be described in a day-night cycle as MIG = $f(t,z)\partial Z_p/\partial z$, where $f(t,z)$ is time and space varying vertical migration velocity. PRED$_p$ represents the losses incurred by $Z_p$ as a result of predation. PRED$_p$ is the only component of the source function which is strongly dependent on the state of turbulent mixing, as has already been mentioned. Its magnitude can be determined from the biomass of predator $B$ on the assumption that the loss incurred by the prey concentration $Z_p$ is proportional to the increase in the predator biomass (here PRED$_p$ = $gB/W_p$ where $g$ is the predator growth rate (see Eq. 5) and assumed $\alpha=5/3$; this means that 60% of ingested food is contributed to predator growth and 40% is released as fecal pellets and excreted material which it is assumed to be lost immediately). Equation for predator is also the diffusion equation and can be described by equation (4) considering the combined effects of dissipation and increased encounter velocities due to physical diffusion together with variable growth:

$$\frac{\partial B}{\partial t} = \frac{\partial}{\partial z} \left( K_z \frac{\partial B}{\partial z} \right) + gB - \text{PRED}_B \tag{4}$$

where PRED$_B$ is the predation by higher order predators, but this term here is not included (PRED$_B$ = 0). Predator growth rate, $g$, is linearly related to encounter rate, $E$, by:

$$g = g_1 E + g_2 \quad \text{for} \ Z < Z_{\text{max}}$$

$$g = g_{\text{max}} \quad \text{for} \ Z \geq Z_{\text{max}} \tag{5}$$

where $g_1$ is the proportionality parameter between growth rate and encounter rate and $g_2$ is the constant growth rate term. Increased encounter rate only leads to increased growth when the predator is food limited and then the first term of Eq. (5), $g_1E$, has decisive influence on growth rate; if the mean time between prey encounter becomes small, the predator growth rate becomes limited not by prey availability, but by the parameter $g_2$ and then the predominant influence has $g_1$ and $g_2 \to g_{\text{max}}$.

These coefficients may be assumed as constants (Davis et al. 1991). The encounter rate, $E$, between predator and prey, can be derived from the equation (Rothschild and Osborn 1988; Kiorboe and Saiz 1995; Seuront et al. 2001):

$$E = \pi Z_p d^2 \frac{u^2 + 3v^2 + 4w^2}{3(v^2 + w^2)^{0.5}} \tag{6}$$

where $d$ is the predator’s contact radius (i.e. the maximum distance at which the predator can perceive prey), $Z_p$ is the prey concentration, $u$ and $v$ are speeds of the
prey and the predator, respectively, and \( w \) is turbulent velocity (also called turbulent encounter velocity and encounter velocity) at a particular separation computed by Rothschild and Osborn (1988):

\[
w = 1.9 \left( \frac{\epsilon l}{10} \right)^{1/3}
\]  

(7)

where \( l \) is the characteristic length scale of turbulent eddies.

3. TURBULENT DIFFUSION

The fine structure dynamics are reflected in equations for marine plankton by means of the coefficient of turbulent diffusion of a passive substance, \( K \), on the assumption that vertically intermittent layers are horizontally homogeneous. The problem of the analytical definition of the coefficient \( K \) has not yet been resolved and continues to be a research subject for hydrophysicists and oceanographers. The latter have attempted to find a formula for this coefficient not only empirically but also on the basis of the theory of similarity. It seems that the best of them to date is the fundamental approach formulated by Osborn (1980):

\[
K(z) = \Gamma \varepsilon N^2(z)
\]  

(8)

where \( N \) is the Väisälä-Brunt parameter and \( \Gamma \) is an efficiency coefficient taking various values: according to Gregg (1989), \( \Gamma = 0.2 \), and according to Osborn himself (Osborn 1980).

This formula (Osborn 1980) determines the coefficient \( K \) for stable-stratified density distribution (the density distribution in the water is absolutely stable). But \( \varepsilon \) as well as \( N \) depend on the vertical gradient of density and turn over (inverse).

Various publications quote different formulas expressing the rate of energy dissipation, \( \varepsilon \), and transform this expression by means of different parameters. But, in this paper, \( \varepsilon \) was assumed after Dower et al. (1997):

\[
\varepsilon = 5.82 \times 10^{-9} \frac{U_{10}^3}{z}
\]  

(9)

Here, the energy dissipation given by the Eq. (9) is used for \( z > 1/3H_s \), where \( H_s \) is the significant wave height. However, for \( z < 1/3H_s \), \( \varepsilon \) is constant according to Young and Banner (2001). The significant wave height is a function of wind speed (Massel 1996):

\[
H_z = 1.6 \times 10^{-3} \frac{U_{10}^2}{g} \left( \frac{gX}{U_{10}^2} \right)^{0.5}
\]

where \( g = 9.81 \text{ m s}^{-2} \) and \( X \) is a wind fetch.

Assuming \( X = 100 \text{ km} \) we get: \( H_z = 0.8 \text{ m} \) for \( U_{10} = 5 \text{ ms}^{-1} \), \( H_z = 1.62 \) m for \( U_{10} = 10 \text{ ms}^{-1} \), \( H_z = 2.42 \) m for \( U_{10} = 15 \text{ ms}^{-1} \) and \( H_z = 3.23 \) m for \( U_{10} = 20 \text{ ms}^{-1} \). In the upper part of the surface mixed layer, \( \varepsilon \) reaches large values \( (\varepsilon = 17.46 \times 10^{-9} U_{10}^3/H_z, \text{for} z<1/3H_z) \), which falls substantially with depth according to Eq. (9) for \( z > 1/3H_z \); however, in the lower layer, this decrease gradually declines.

The rate of energy dissipation is suppressed by work of density uplift forces represented by the Väisälä-Brunt frequency which depends on the density distribution:

\[
N^2 = \frac{g}{\rho} \frac{\partial \rho}{\partial z}
\]  

(10)

Substituting Eqs (9) and (10) to the equation (8) we’ll get formula for the coefficient of vertical diffusion, but it sufficiently fulfils the requirement of our modelling.

The intensity of turbulent mixing can be simulated by superimposing on the wind velocity a variable structure of the vertical gradient of density. Turbulent diffusion, \( K \), is here related to surface wind speed, \( U_{10} \), through the turbulent kinetic energy dissipation rate, \( \varepsilon \), after Osborn (1980). Fig. 1 demonstrates the physical diffusivity, as a function of depth at two wind velocities \( (U_{10} = 4 \text{ and} 8 \text{ ms}^{-1}) \) for three mean vertical gradients of density, \( \partial \rho/\partial z = 0.00001, 0.0001, 0.0005 \text{ kg m}^{-1} \), and taken from relationship equation (8). Physical diffusivity increases as a cubic function of wind speed and decreases with increasing depth through energy dissipation rate. In the upper of the surface mixed layer of sea,
K reaches very large values which fall substantially with depth according to equation (8); but in the lower layer, gradual decline in $K$ is observed. Physical diffusivity decreases as a inverse square function of the Väisälä-Brunt parameter; hence, any increase in vertical gradient of density causes the intensity of turbulent mixing to decline.

4. RESULTS OF THE NUMERICAL CALCULATIONS

The investigations of the effect of small-scale interlayers on the field of zooplankton (prey and predator) in the sea were carried out on the basis of the mathematical model presented above. The system of equations (1) – (4) with initial and boundary conditions (see Appendix 2) has been solved numerically using a Crank-Nicholson indirect method (Potter, 1982) in an area of $0 \leq z \leq 20$ m by digitising this region with a variable step and with a time step of 7.5 min. This method is absolutely convergent and is characterized by a second order accuracy with respect to the time and space discretization step. The detailed algorithm of the solution to the type model can be found in Dzierzbicka-Głowacka (2000).

The program of numerical calculations was prepared in such a way that at any given time $t$ and at an arbitrary depth $z$ it allows:

- changing the space step;
- assigning unsteady conditions;
- changing the duration of unsteadiness.

The program thus allows rapid simulation of physico-biological conditions of the investigated basin. Empirical data for the calculations were taken from the literature for Gdansk Gulf (Witek 1995).

By solving the set of equations (1) – (4) and the assumptions made we can obtain a simulated variability of vertical distributions of prey, $Z$, and of predator, $B$, biomass in time along depth.

The following assumptions were made in the calculation: 1) *Pseudocalanus minutus elongatus* center for latest development stages (adult) was used as prey, and *Mysis mixta* center for earlier stages (nauplius) as predator; 2) growth and development of *Pseudocalanus* spp. was obtained by Dzierzbicka-Głowacka (2004) and here considered for high level of food concentration which does not influence on physiological processes; mean weight of prey was assumed $W_{\text{prey}} \approx 0.1 \text{ mg wet}$, it corresponds to 6.4 µgC (Winogradow and Szuszkina, 1987); 3) growth rate of $0.5$–$1.5 \text{ mg wet size class of } Mysis mixta$ was given by Witek (1995) as $0.05 \text{ mgwet wt d}^{-1} (0.071 \text{ d}^{-1})$; here assumed that mean weight of predator is equal to ca. 160 µgC and mean length is equal to $d_o \approx 10 \text{ mm}$; 4) swimming speed of predator, $v$, was derived by Miller et al. (1988) as: $\log v (\text{cm s}^{-1}) = 1.07 \log d_o (\text{mm}) - 1.11$; 5) swimming speed of zooplankton prey, $u$, was based on the estimated of Sundby and Fossum (1990) who used an average speed of 0.5 body length for *Calanus finmarchicus* nauplii; hence, here prey swimming speed, $u$, for mean length 1 mm was 0.05 cm s$^{-1}$; 6) the perception distance for predator, $d$, was based on the estimate of Laurence (1985) as $d = 2/3\pi(0.75d_o)^2$; 7) the characteristic length scale, $l$, was defined as the predator’s reactive distance; hence the separation distance between predator and prey
is also the perceptive distance of the predator (i.e. \( l = d \) in equation (7)); 8) the initial values of prey concentration and predator biomass were assumed as \( Z_p = 10^3 \) ind. m\(^{-3}\) and \( B = 800 \) µgC m\(^{-3}\); (9) assumed \( f(t,z) = 0 \), where this function describes time and space varying of vertical migration velocity, because adult \( P. \ elongatus \) slightly move in diurnal cycles in the upper layer of investigated aquatic basin.

The combined effect of correct scaling, \( l \), body length, \( d_0 \) and velocity of predator, \( v \), and prey concentration, \( Z_p \), for turbulence on the predator-prey encounter rate, \( E \), and the growth rate of predator, \( g \), was in detail described by Dzierzbicka-Głowacka (2006).

Taking into consideration earlier assumptions, growth rate of predator, \( g \), as a function of depth for two values of wind speed was here obtained and is shown in Fig. 2. Predator growth rate dependent mainly on encounter rate \( E \). Encounter rate attains the highest values in the upper layer, which fall with depth according to dissipation by the turbulent velocity.

The results of the numerical investigations of the influence of the assumed dynamic conditions characterizing the investigated basin on the function of zooplankton (prey and predator) distribution in this basin are presented graphically in Figs 3–8. The numerical analysis was performed for 2 days with a steady wind of various velocities.

Fig. 3 presents the changes in value of prey concentration and predator biomass with depth at three wind speeds (\( U_{10} = 2, 4 \) and \( 8 \) ms\(^{-1}\)) for three values of the vertical gradient of density \( \partial \rho / \partial z \) (0.00001, 0.0001 and 0.0005 kg m\(^{-4}\)) at \( t = 48 \) h. The vertical distributions of \( Z \) and \( B \) are significantly
influenced by turbulent processes in the surface mixed layer. The predicted effect of turbulence on the variability of the characteristics investigated is much more pronounced in case when $U_{10} = 8 \text{ m s}^{-1}$ than when $U_{10} = 2$ and $4 \text{ m s}^{-1}$.

The effect of density gradient on the vertical distributions of $Z$ and $B$ rises with increasing wind speed. Any increase in wind speed causes a rise in predator biomass, through an increase in predator growth rate (Dzierzbicka-Głowacka, 2006), and a fall in prey concentration, through an increase in predation which is proportional to predator biomass (see section 2). The results of numerical simulations described here indicate that, in the upper of the surface mixed layer ($z < 1 \text{ m}$ for $U_{10} = 2 \text{ m s}^{-1}$; $z < 1.5 \text{ m}$ for $U_{10} = 4 \text{ m s}^{-1}$ and $z < 3 \text{ m}$ for $U_{10} = 8 \text{ m s}^{-1}$), the distributions of predator biomass increase with rising the vertical gradient of the density. At higher depth ($z > 2 \text{ m}$ for $U_{10} =$

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**Fig. 4.** The influence of the occurrence of a fine mixing interlayer of $\Delta h = 0.5 \text{ m}$ thickness in a stable structure of turbulently stirred water masses (C) at vertical distributions of temperature (A) and salinity (B) on the physical diffusivity $K$ (in $\text{m}^2 \text{s}^{-1}$) (D) at the wind speed: $U_{10} = 4 \text{ m s}^{-1}$. 
2 ms⁻¹; z > 4 m for \( U_{10} = 4 \) ms⁻¹ and z > 9 m for \( U_{10} = 8 \) ms⁻¹), \( B \) is inversely related to the density gradient. However, at intermediate depth (1 < z < 2 m for \( U_{10} = 2 \) ms⁻¹; 1.5 < z < 4 m for \( U_{10} = 4 \) ms⁻¹ and 3 < z < 9 m for \( U_{10} = 8 \) ms⁻¹), the effect of the density gradient on \( B \) could not be assessed from these data (see Fig. 3A). For the concentration of prey, this situation is reverse, namely in the upper layer, \( Z_p \) was inversely related to the vertical gradient of the density; however, in the lower one, \( Z \) decreases with declining the density gradient (see Fig. 3B). The differences in distributions of prey concentration as well as of predator biomass for different values of the mean density gradient decline with depth.

Keeping this in mind, let us assume that laminar interlayer of the \( \Delta h = 0.5 \) m thickness appears at \( t = 44 \) h in turbulently mixed layer. Fig. 5 shows the results of simulations performed under the assumption that \( U_{10} = 4 \) ms⁻¹, \( \rho \) and \( K \) are given in the form of the distributions shown in Fig. 4C and 4D, and the time of action of the hydrodynamic sources of mixing \( t = 60 \) min. and 120 min. The simulation studies with the numerical model described above are carried out with real, vertical distributions of temperature and salinity (Figs 4A and B). A station located closer to the Vistula river outlet in the southern part of the Gdansk Gulf has been chosen to investigate the effect of small-scale interlayers on the time-dependent vertical distributions of marine zooplankton concentration field. In spring, a visible, short-lasting (even a few hours) drop in the salinity (even to 2‰ in 1998) and rise in the temperature (to 11°C) of surface waters takes place at this station. This situation is caused by an inflow of waters from the Vistula river. During the inflows of warmer waters, the thermocline began to form, salinity decreases, reaching in May, in the surface layer, values near 4‰. The further from the Vistula river outlet, the smaller and smoother is the variation of vertical structure of temperature and salinity caused by horizontal diffusion.

The distribution curves in Fig. 5 illustrate the state of the concentration field in time of appearance of the laminar layer (Fig. 5A), after a time \( t = 60 \) min. (solid black line) and \( t = 120 \) min. (solid grey line) and after a time 60 min. (chain dashed line) from the instant hydrodynamic instability occurred. During the entire experiment \( Mysis mixta \) – predator “feeds on” \( P. minu-
Fig. 6. The concentration field $B_0$ and $Z_0$ in time of appearance of the laminar layer (A); Evolution in time of vertical distributions of predator biomass $B$ (in $\mu$gC m$^{-3}$) (B) and prey concentration $Z$ (in ind. m$^{-3}$) (C) under conditions of wind speed $U_{10} = 2$ ms$^{-1}$ and occurrence of a laminar layer in stable structures of $\Delta h = 0.5$ m thickness when the duration time interlayering $t_t = 60$ min. (black) and 120 min. (grey).

Fig. 7. The concentration field $B_0$ and $Z_0$ in time of appearance of the laminar layer (A); Evolution in time of vertical distributions of predator biomass $B$ (in $\mu$gC m$^{-3}$) (B) and prey concentration $Z$ (in ind. m$^{-3}$) (C) under conditions of wind speed $U_{10} = 8$ ms$^{-1}$ and occurrence of a laminar layer in stable structures of $\Delta h = 0.5$ m thickness when the duration time interlayering $t_t = 60$ min. (black) and 120 min. (grey).
The opposite manner. The decrease or increase of the concentration of prey develops in the concentration distribution as a result of an increase of predation; i.e. the decrease in prey concentration as a result of an increase of predation; i.e. the concentration of prey develops in the opposite manner. The decrease or increase of the concentration values reaches ca. ±1.2% of the value in a vertically uniform basin for prey and ±3.5% for predator, for \( t = 120 \text{ min.} \) In light of hydrodynamics principles, such an irregularity occurs when a resultant force different from zero acts on a zooplankton cell. When the force of gravity is greater than hydrostatic lift, a zooplankton cell will sink at different rates in a laminar or turbulent layers. Figs 6 and 7 show an irregularities as above in fine-scale heterogeneities in distributions \( B \) and \( Z \) under the influence of two different \( U_{10} = 4 \text{ ms}^{-1} \) values of wind speed i.e. \( U_{10} = 2 \text{ ms}^{-1} \) (Fig. 6) and \( 8 \text{ ms}^{-1} \) (Fig. 7), where the changes in the distribution of \( Z \) and \( B \) are ca. ±0.9% and ±1.2% for \( U_{10} = 2 \text{ ms}^{-1} \) and ±3% and ±6% for \( U_{10} = 8 \text{ ms}^{-1} \), respectively. A decrease in the wind speed causes that the decrease in predator biomass inside the layer of density fluctuation drops (Fig. 6). However, the increase in the wind speed causes reverse situation; this means that the decrease in predator biomass inside this layer rises. These simulations have shown that fine-scale stratification in the concentration fields \( B \) and \( Z \) depend largely on the state of the turbulent mixing processes in the layers through the vertical distribution of density and wind speed.

Figs 5, 6 and 7 also present exemplary calculations illustrating the effect of the duration of the disturbance on the characteristics investigated in the case of a laminar layer of \( \Delta h = 0.5 \text{ m} \) thickness, situated at a depth \( z = 2 \text{ m} \) and \( U_{10} = 4, 2 \) and \( 8 \text{ ms}^{-1} \). However, fine-scale stratification in its concentration field only begins to appear after a time \( t = 60 \text{ min.} \), becoming the more distinct, the longer the source of hydrodynamic mixing lasts. These Figures show the increase in physical diffusivity and the increase in fine-scale heterogeneities in distributions \( B \) and \( Z \) under the influence of an increase in the wind speed. An increase in dissipation while the wind speed rises, causes that laminar mixing processes increase in intensity. The calculations suggest that an irregularities in the concentration field of \( B \) and \( Z \) caused by laminar stratification of the density is in equilibrium for \( U_{10} = 4 \text{ ms}^{-1} \) and at a depth \( 1.5 < z < 4 \text{ m} \), i.e. an increase and a decrease in \( B \) and \( Z \) is in more or less just the same taking into consideration above set of model parameters. If a disturbance appears above this depth, larger decrease in predator biomass is observed (as in case of \( U_{10} = 8 \text{ ms}^{-1} \)); however, beneath one, this drop in \( B \) falls (as in case of \( U_{10} = 2 \text{ ms}^{-1} \)). However, for \( U_{10} = 2 \) and \( 8 \text{ ms}^{-1} \), a boundary depth, at which an irregularities in concentrations \( B \) and \( Z \) are in equilibrium, is at \( 1 < z < 2 \text{ m} \) and \( 3 < z < 9 \text{ m} \), respectively. On the basis of the results of the numerical simulations we can deduce that when \( tt < 60 \text{ min.} \), fine-scale interlayering is completely mixed in investigated case.

The evolution of the vertical distribution of zooplankton biomass field (prey and predator) has been determined for a uniform turbulent medium (for \( U_{10} = 4 \text{ ms}^{-1} \)) in which a laminar interlayer of \( \Delta h = 1 \text{ m} \) thickness, lasting for \( t = 60 \) and 120 min., appears (see Fig. 8). The numerical results, in this case, show similar structural changes in vertical distributions of \( Z \) and \( B \) to these were observed in the case when \( \Delta h = 0.5 \text{ m} \). Visible anomalies in the characteristic investigated appear, which intensity is less than in the case when \( \Delta h = 0.5 \text{ m} \). This study reveals that the thicker the layer, the smaller the structural anomaly. The calculations also suggest that layers of thickness \( \Delta h > 1 \text{ m} \) do not generate a significant effect on the characteristics investigated.

The distributions presented in all Figures illustrate the disappearance of the effect of structural anomaly on the prey and predator biomass after termination of the disturbance. The disappearance of this ef-
fect is monotonic in time, after a few hours (dependent on wind speed) the vertical distribution of \(Z\) and \(B\) does not reveal a step non-uniformity in its structure.

Fig. 8. The influence of the appearance of a laminal layer of the thickness \(\Delta h = 1\) m in stable structure on the vertical distribution of predator biomass \(B\) (in \(\mu\text{gC m}^{-3}\)) (A) and prey concentration \(Z\) (in ind. m\(^{-3}\)) (B) when \(t_t = 60\) min. (black) and 120 min. (grey) and \(U_{10} = 4\) m\(\text{s}^{-1}\).

5. CONCLUSIONS

The one-dimensional model of diffusion of marine plankton presented here can be utilized for numerical investigations on space-time changes in the vertical distribution of prey and predator concentration field. The paper does not report experimental results; rather, it gives an analysis of effect of mechanism of turbulent mixing processes in the intermittent fine structure on the distributions of investigated characteristics.

The calculations were made for the given vertical distribution of density at different values of the wind velocity.

The results of the numerical investigations, achieved on the basis of 1D-model, indicate that intensity of the layer-mixing processes depends on the vertical distribution of density (i.e. on the vertical gradient of density and thickness of the intermittent fine structure), the time of action of hydrodynamic sources of mixing and the wind speed.

An increase of wind speed, which causes a rise in predator biomass as a result of an increase of predator growth rate, also brings about an increase of effect of fine-scale interlayering on the vertical distribution of predator biomass. The changes in the distribution of predator biomass induce opposite changes in the distribution of prey concentration, because the loss in the prey concentration is proportional to the increase in the predator biomass through predation; i.e. the higher predator biomass, the stronger predation or the lower prey concentration.

On the basis of the studies of the numerical simulations for investigated case we can deduce that for low values of wind speed \((U_{10} < 2\) m\(\text{s}^{-1}\)) and for short time of action of hydrodynamic sources of mixing \((t_t < 60\) min\.), fine-scale interlayering is not created. However, for higher values of wind speed and longer duration of the disturbance (even a few hours), the changes in the distributions of \(B\) and \(Z\) caused by laminar stratification of the density are visible and can be at the order of a few and a dozen or so percentage of the initial value. For instance, for \(U_{10} = 12\) m\(\text{s}^{-1}\) and \(t_t = 240\) min., a decrease or an increase of the values of the characteristics investigated is equal to ca. 25\% for predator biomass and
ca. 11% for prey concentration (Fig. 9). For high values of wind speed, an increase or a decrease of the concentration values will not drive at infinity, because an increase in predator biomass will gradually drop as a result of a decrease in prey concentration which is caused by an increase of predation; however, this decrease in prey concentration causes a fall in encounter rate between predator and prey (see Eq. 6).

The calculations also suggest that the intensity of turbulent mixing sources decreases with increase in thickness of the layer. The presented results of numerical investigations concerning the effect of dynamic processes on the shape and absolute value of the vertical distribution of prey concentration and predator biomass field reveal that these processes are responsible for the shape of vertical profiles of investigated characteristics to the same extent as predator growth rate. The simulation studies of the effect of chemical and dynamic processes on the vertical distribution of chlorophyll-\(a\) concentration given by Druet and Zieliński (1994) shown that these processes are responsible for the observed in situ shape of vertical profile of phytoplankton concentration to the same extent as solar energy influx.

The presented calculations show that the fine structure dynamics has less effect on the vertical distribution of zooplankton (prey and predator) concentration than in the case of phytoplankton concentration. However, it is difficult to establish which of the mentioned processes prevails and to what extent it limits the shape of the distribution of marine plankton concentration at depth. Decisive processes of physical and biological controlling of these distributions are equally important. Their intensity depend on forcing data (meteorological, physical and biological) as well as the detailed descriptions of the various relationships between the rates of physiological processes of the species and environmental factors.

6. REFERENCES


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APPENDIX 1

Parameters of the Eq. (1)

The temporal changes in weight are caused by ingestion $ING$, zooplankton fecal pellets $FEC$, and metabolism $MET$. The ingestion rate $ING$ is defined as the rate of intake per unit time per animal, the coefficient of food selection being given by $\tau$. This function $fil(\{Phyt\})$ with the maximal ingestion rate $f_{max}$ is a function of both the food concentration $\{Phyt\}$ and the animal’s weight $W_p$, and takes a value of $\frac{2}{3}$ (Paffenhöfer, 1971). The total metabolic loss $MET$ can be split into three components with different relations to the food uptake rate $ING$. $M_z$ is assumed to be the resultant or basic metabolism, independent of food supply. The respiratory costs of foraging and capturing food $M_z$ should fall as the food concentration and, correspondingly, $fil(\{Phyt\})$, rises. Finally, there is the cost of assimilation and biochemical transformation of the food (specific dynamic action, $M_a$), proportional to $A$ with percentage of ingestion regenerated as soluble excretion zooplankton $n_i$ (Steele and Mullin 1977). The rate of assimilation $A$ is computed as a constant fraction of the ingestion rate (e.g. Steele (1974) who used $A = 0.7$ $ING$). Fecal pellet production is proportional to $ING$ with percentage of ingestion egested as fecal material $nf$.

$$ING = \tau \cdot fil(\{Phyt\}) W_p \alpha \quad (1.1)$$

$$fil(\{Phyt\}) = f_{max}^{-1} (\{Phyt\} - \{Phyt\}_o) / (\{Phyt\}_o - \{Phyt\}_o)$$

$$MET = M_z + M_r + M_a = M_z + n_i A, \quad A = n_i ING \quad (1.3)$$

$$FEC = n_f ING \quad (1.4)$$

APPENDIX 2

Initial and boundary conditions.

The following initial and boundary conditions supplement equation system (1) – (4): the initial vertical distributions of prey and predator are known:

$$W_p(z, 0) = 6.4 \, \mu g C \quad 0 \leq z \leq H$$

$$Z_p(z, 0) = 10^3 \, \text{ind. m}^{-3} \quad 0 \leq z \leq H$$

$$Z_o(z, 0) = W_p(z, 0) Z_p(z, 0) \quad 0 \leq z \leq H$$

$$B_o(z, 0) = 800 \, \mu g C \quad 0 \leq z \leq H \quad (2.1)$$

The vertical gradient of prey and predator concentration flux are zero at the sea surface ($z=0$) and the sea bottom ($z=H$):

$$F_z(0) = \hat{K}_z \frac{\partial Z(z,t)}{\partial z} \bigg|_{z=0} = 0 \quad F_g(0) = \hat{K}_z \frac{\partial B(z,t)}{\partial z} \bigg|_{z=0} = 0 \quad (2.2)$$

$$F_z(H) = \hat{K}_z \frac{\partial Z(z,t)}{\partial z} \bigg|_{z=H} = 0 \quad F_g(H) = \hat{K}_z \frac{\partial B(z,t)}{\partial z} \bigg|_{z=H} = 0$$

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