Physical oceanography and marine ecosystems: some illustrative examples*

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SUMMARY: The role of physical oceanography on different length and time scales in marine ecosystems is elucidated by means of some illustrative examples. Special focus is put on time and length scales, physical mechanisms underlying production and distribution of biological matter, contact rate and small-scale turbulence, vertical migration and larval settlement in tidal flow and the influence of advection on the distribution of plankton and fish eggs.

Key words: physical mechanisms, length and time scales, advection, turbulence, tidal flow, contact rate, migration, settlement.

INTRODUCTION

It is well known that there is a close relationship between physical and biological processes in the ocean. However, despite this knowledge, it is surprising that physical oceanography still plays a very modest part in some marine biological milieu. We therefore believe that there is a need to stimulate more cooperation between physicists and biologists to prevent future marine scientific programs which suffer due to lack of cooperation.

Lack of integration of physical oceanography in biological investigations often has economical reasons. Ecological field experiments are time consuming and costly and biologists are tempted to limit the physical oceanographic part to a minimum and make “a best guess” based on e.g. a few CTD-stations. Such data, however, tells usually next to nothing about the physical processes which are necessary to interpret the biological data in a satisfactory way.

It is usually decisive that the physical data are sampled simultaneously with the biological data. This is especially important in areas with strong gradients where the processes take place on small time and space scales, e.g. in fronts, current shear, upwelling.

The possibility of cooperation in field experiments has been facilitated in recent years. Work is in continuous progress on the development of instruments which have improved the measuring technique and increased the efficiency of data sampling, which has therefore become considerably less time consuming than just a few years ago. Some of the biological data may today be collected with a coverage and resolution comparable with the best physical data. Also the development of ecological models (coupled hydrodynamical and biological models) have been an inspiration for cooperations.

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LENGTH AND TIME SCALES

The nature of the relationship between physical and biological processes is very complex. Both rely on solar energy, biologically through photosynthesis and physically, direct through heating of the water and indirectly as momentum transmitted to the ocean surface from the wind. An appropriate way to approach the subject is to get a feeling for the length and time scales of the organisms and phenomena to be discussed. Fig. 1 shows some characteristic size range of organisms and physical length scales and time scales for some physical and biological features. Somewhat simplified, it seems that while physical features determine the spatial scales of ecological processes, the organisms determine the time scales: e.g. from the baroclinic Rossby radius of deformation which is the typical width of coastal upwelling areas and ocean currents to the biologically important mixed layer depth ($\approx 10^2$ m) to the viscous length (Kolmogoroff length) in the lower end of the scale ($\approx 10^{-2}$ m) where viscosity starts to smooth out turbulent fluctuations. The time scale may range from 100 years, the life span of a mammal, to a few years for fish and further to hours, the doubling time of bacterias.

SOME PHYSICAL MECHANISMS UNDERLYING PRODUCTION AND DISTRIBUTION OF BIOLOGICAL MATTER

It may be appropriate to start with a description of some important mechanisms which govern production and transport of biological matter in the ocean. The main mechanisms in this respect are advection, turbulent diffusion, wind mixing, the tide and tidal fronts, Ekman pumping, upwelling and convection processes due to evaporation or surface cooling and freezing. The significance of the different mechanisms varies both in time and geographically.

Turbulence

Shear-generated turbulence

As a rule of thumb production of turbulence takes place in a vertical current shear when the gradient Richardson number is less than $1/4$ (Miles, 1961):

$$R_i = \frac{g \frac{\partial \rho}{\partial z}}{\rho \left( \frac{\partial u}{\partial z} \right)^2}$$ (Richardson number)
where \( \rho \) = density, \( g \) = acceleration of gravity, \( u \) = horizontal velocity and \( z \) = vertical coordinate.

Furthermore,

\[
\frac{g}{\rho} \frac{\partial \rho}{\partial z} \quad \text{(shear stress)}
\]

represents the destabilizing force and \( \left( \frac{\partial u}{\partial z} \right)^2 \) represents the stabilizing force and \( \left( \frac{\partial u}{\partial z} \right)^2 \) represents the destabilizing force (see Fig. 2). Even for weak current shear the conditions for turbulence production may be present when the stratification is weak. The vertical shear is usually strongest in the surface and bottom layers which are thus the main areas for shear generated turbulence in the ocean.

Production of turbulence in a stratified fluid is not a continuous process but usually has an intermittent character. The turbulence appear as “bursts” in depth levels with very low Richardson number. In the depth levels where the “bursts” appear the water is strongly mixed and the stratification may change considerably. After some time new conditions favourable for “burst” generation are built up again and turbulence is generated.

An example illustrating the effect of the intermittency character of turbulence on the stratification is shown in Fig. 3. The vertical profiles of density and velocity are sampled once every hour at a station

![Fig. 2. – Shear generated turbulence in a stratified fluid.](image)

![Fig. 3. – Velocity (––––) and density (------) profiles from Station H in Fig. 18a. The numbers are bulk Richardson numbers.](image)
about 3 km from the outlet of a power plant situated at the head of a narrow fjord (Hylsfjorden) on the west coast of Norway (see Fig. 18a). The density is calculated based on CTD data sampled from a ship, anchored near a buoy rig at Station H1 carrying seven SD-2000 current meters in 1, 2, 3, 4, 5, 6, and 7 m depth respectively. The width of the fjord at the station site is about 1 km. The discharge from the power plant was 200 m$^3$ s$^{-1}$. There was no wind or precipitation during the experiment and the tide was very weak in the fjord. It is seen in the figure that the changes in the stratification was much more pronounced in the depth levels with very low values of the Richardson numbers (the numbers are bulk Richardson number).

**Breaking of internal waves**

A well known source of turbulence is related to internal wave activity. Turbulent energy is transferred from the waves when the waves become unstable and break either in the interior of the flow or along sloping boundaries (Fig. 4). A condition for generation of internal waves is that the water-masses are stratified. Consequently, the contribution of turbulent energy from this source varies with time, especially at higher latitudes. A typical example is the Barents Sea. In summer and autumn, when the ocean is stratified, internal wave activity may contribute to the turbulent energy level in parts of the Barents Sea, while in winter when the water masses are almost homogeneous this source is absent.

**Wind generated turbulence**

Wind energy supplied to the surface is transferred to turbulent energy by two main mechanisms: shear instabilities as described above and breaking of surface waves. The latter usually injects turbulent energy at a much smaller scale than the former (e.g. Phillips, 1966). There is however an exception. When Langmuir circulations appear, which are driven by breaking waves, mixing takes place on much larger scales than individual wave-breaking events.

**Mixing caused by tides**

Mixing related to tidal action is especially important in shelf waters and has a marked periodic character related to the tidal cycle. Mixing due to tidal currents show small variations between each tidal cycle in shelf areas where the difference between spring and neap tides is small. However, some areas have a very pronounced spring-neap tidal cycle as e.g. the south Australian Shelf where there is almost no mixing at neap tide while at spring tide the water masses are exposed to strong mixing (Provis and Lennon, 1983). Simpson and Hunter (1974) suggested that the marked frontal structure occurring on the shallow European continental shelf during the summer months is produced by variations in the level of tidal mixing (Fig. 5). The location of the fronts is essentially determined by the parameter Q, which is heat flux.

![Fig. 4.](image1.png)  
*Fig. 4. – Breaking internal waves a) in the interior of the flow (left) and b) along a sloping bottom (right).*

![Fig. 5.](image2.png)  
*Fig. 5. – Front caused by tidal mixing. Q is heat flux.*
of a given area must be replaced by water which is "sucked" vertically up into the surface layer (Fig. 7). The suction may take place in connection with slowly moving or quasi-stationary cyclons over an ocean area.

Applying the Ekman mass transport equations (see Gill, 1982):

\[
\rho \left( \frac{\partial U_E}{\partial t} - f V_E \right) = T_x \\
\rho \left( \frac{\partial V_E}{\partial t} + f U_E \right) = T_y
\]

\((T_x = \rho C_D W_x^2, T_y = \rho C_D W_y^2; W_x \text{ and } W_y \text{ are wind velocity components})\) and the integrated equation of continuity:

\[
\int_0^z \left( \frac{\partial U}{\partial x} + \frac{\partial V}{\partial y} + \frac{\partial W}{\partial z} \right) dz = 0
\]

\[
\Rightarrow \frac{\partial U_E}{\partial x} + \frac{\partial V_E}{\partial y} - W_E = 0
\]

and assuming stationary conditions, the Ekman volume transport is:

\[
U_E = \frac{1}{\rho f} T_y \\
V_E = -\frac{1}{\rho f} T_x
\]

Then for a stationary or slowly moving low over the ocean the Ekman suction velocity, \(W_E\), is:

\[
W_E = \frac{1}{\rho f} \left( \frac{\partial T_y}{\partial x} - \frac{\partial T_x}{\partial y} \right)
\]

The two terms in the bracket represent the curl of wind stress. Applying monthly mean wind stress data for November in the Barents Sea (Martinsen et al., 1992), we got a vertical velocity 0.01 - 0.03 cm s\(^{-1}\), or water "sucked" vertically about 10-30 m day\(^{-1}\).

Since the phenomenon described is closely related to slowly moving wind fields such events are rather episodic.

**Coastal upwelling**

A wind blowing along a coast in the northern hemisphere with the coast to the left of the wind direction causes a transport of upper layer water out from the coast, so called Ekman drift (e.g. Gill, 1982; Cushman-Roisin, 1994 and Fig. 8). To compensate
for this water transport, upwelling of usually nutrient rich water takes place along the coast. The interface between the waters upwelled along coast and the offshore waters constitutes an upwelling front (Fig. 8). The amount of water (the depth of the water column) which is affected by the upwelling and the position of the front depends on the stratification and the strength of the wind. Readers who are not familiar with this general subject are referred to the volume edited by Richards (1981).

Upwelling in fronts

A frequent phenomenon in the ocean are the appearance of quasi-geostrophic fronts where a pressure gradient perpendicular to the front drives a current parallel to the front. Due to the friction in the water the pressure gradient and the Coriolis force are not exactly balanced (quasi-geostrophic) causing divergence to the left of the center of the front and convergence to the right with a resulting vertical flow between. For details about this process, see Garret and Loder (1981).

Upwelling along an ice edge

Along an ice edge upwelling may also take place caused by wind stress which exerts different stresses on ice and open water which cause the moving ice to exert stress on the ocean beneath. If the seawater is homogeneous or weakly stratified the vertical transport may affect a considerable part of the upper water masses and transport water vertically 10-20 m day$^{-1}$. For more details the reader is referred to Häkkinen (1990).

Thermal convection and convection due to sea ice formation

Convection caused by cooling of the surface and sea ice formation takes place in high latitudes, in the Arctic and Antarctic. Due to intense surface cooling convective mixing may reach great depths during the winter. When sea ice is formed, salt brine drains out and increases the density of the underlying water. This in turn triggers convection which may reach great depths.

Deep water formation may also be caused by other mechanisms as in the Eastern Mediterranean. Evaporation due to heating of the surface increases the salinity of the surface layer water thus preconditioning the formation of Mediterranean deep water due to winter-time heat loss.

SOME EXAMPLES OF RELATIONSHIPS BETWEEN PHYSICAL AND BIOLOGICAL PROCESSES IN THE OCEAN

It is not possible in a short article to cover all aspects related to physical-biological processes in the ocean. I will therefore limit the presentation to a few subjects where it is obvious that thorough knowledge of the physical processes is crucial to understanding the biological processes. (Two of the subjects, 1 and 3, are closely related to the topic of this volume).

The subjects are the following:
1. Plankton contact rate and small-scale turbulence.
2. Vertical migration in tidal flow.
3. Larval settlement in turbulent tidal flow.
4. The influence of advection on distribution of plankton, cod eggs and larvae.
5. Impact of man-made environmental changes on ecosystems.

The presentation within each subject is mostly based on published papers in the last decennium. Due to lack of reliable field experiments, most of subjects 1 and 3 are based on models, both numerical and analytical.

Plankton contact rate and small-scale turbulence

The first study of the relation between small-scale turbulence and plankton contact rates was an analytical study by Rothshild and Osborn (1988).
Before that time focus was put on some functional studies, in laboratory experiments without turbulence, of the relative density of predator-and-prey plankton. Rothshild and Osborn (1988) estimated the components of predator-and-prey contact that are due to small-scale turbulence. The main results are summarized in Fig. 9, where $v$ is the velocity of the predator, $u$ the velocity of the prey and $w$ the root-mean-square turbulent velocity. As is obvious from the results in the figure, turbulence enhances the contact rates.

The results above are broadly confirmed by Yamazaki et al. (1991), who carried out direct numerical simulation of planktonic contact in turbulent flow. Yamazaki et al. (1991) based their study on the fact that the only way to generate a dynamically correct turbulent field on the scale of planktonic organisms is to simulate the full set of the Navier-Stokes equations directly. The turbulence is generated by a pseudo-spectral method of Rogallo (1981) modified by Squires and Eaton (1990) and the second-order Runge-Kutta method is applied to trace particles in a turbulent flow and simulate planktonic swimming with a random walk. Fig. 10a shows trajectories of three particles in a realistic oceanic turbulence field without random walk (passive particles) and Fig. 10b-d show the same with increasing random walk (active particles). The random walk of the active particles has to be intensified considerably before the effect of the turbulence on movement becomes negligible. As is obvious from the figure, knowledge about the turbulent field is crucial to separate the random walk from the combined effect of random walk and turbulence.

A question which has attracted increasingly attention is illustrated in Fig. 11. Is there a correlation between turbulence intensity and feeding rate of copepods?

The first field study of the influence of turbulence on plankton encounter rates was carried out by

![Fig. 9](image)

**FIG. 9.** – Contours showing the increase in the contact rate as a function of prey velocity ($u$) and predator velocity ($v$) for an uncorrelated rms turbulent velocity ($w$). (Redrawn from Rothshild and Osborn, 1988).

![Fig. 10](image)

**FIG. 10.** – Three-dimensional trajectories of three particles; a) without random walk and c-d) with increasing random walk. (Redrawn from Yamazaki et al., 1991).
Sundby and Fossum (1990). Based on the results from this study and others [MacKenzie and Kiørboe, 1993 (laboratory experiment) and MacKenzie and Leggett, 1993 (model)], Sundby et al. (1994) answered one of the questions which was raised previously in Sundby and Fossum (1990): Is there an optimum level of wind-induced turbulence above which capture of food declines because the relative motion between predator and prey becomes so large that the predator gets too short a time to attack? In their study of encounter rates between first-feeding cod larvae and their prey during moderate to strong wind generated mixing, Sundby et al. (1994) found that the feeding rate increases by a factor of about 7 as wind increases from 2 to 10 m s$^{-1}$. It was concluded that a possible optimal level must be found at higher wind speeds than 10 m s$^{-1}$. The subject is discussed elsewhere in this volume.

**Vertical migration and settlement in tidal flow**

Vertical migration occurs at a variety of periods including tidal periods. There are several reasons for planktonic migration: predation avoidance, bioenergetic advantages and when vertical shear is present, vertical migration may be used to re-establish horizontal position. Vertical migration is usually combined with forced movements related to the flow field: e.g. vertical migration in a sheared, oscillatory tidal current can bring about long-term transport of larvae known as selective tidal stream transport.

A detailed study of migration in such an oscillatory tidal current demand a comprehensive field experiment to determine both the migration of the organisms and the flow field. Up to now, as far as is known by the author, only a few experiments, all of modest extent, have been carried out. Some theoretical studies, however, have been carried out in recent years.

Horizontal motion induced by vertical migration in oscillatory currents were first studied by Hill (1991). His work is an excellent demonstration of a combined effect of a physical and a biological process in the ocean.

Assuming the horizontal velocity $U(z,t)$ of the flow (see Fig. 12):

$$U(z,t) = \frac{U_o z}{h} \sin(\omega t + \phi)$$

and the height of the particle, $z_p(t)$, above the sea bed at any time $t$:

$$z_p(t) = D + a \sin(\omega_m t)$$

where $U_o$ = surface velocity, $h$ = total depth, $\omega$ = angular frequency of the tidal oscillation, $\phi$ = phase angle, $\omega_m$ = angular frequency of the migration, $D$ = mean height of the organism above the sea bed and $a$ = vertical migration amplitude of an individual zooplankter. The velocity of the organism is then:
\[ u_p = U(z_p,t) = \frac{U_c}{h} [D + a\sin(\omega_m t)]\sin(\omega t + \phi) \]

The integration of the equation is straightforward and it is shown that the horizontal displacement provided that \( \omega \neq \omega_m \) lies within the range (see Fig. 13):

\[ x_D \cos(\phi + \epsilon) - A \leq x_p \leq x_D \cos(\phi + \epsilon) + A \]

where \( x_p \) = mean (time-independent) displacement, \( A \) = amplitude of an oscillating time-dependent displacement and \( \epsilon \) = a phase correction.

As is seen in the Fig. 13a,b there is no net long-term horizontal displacement for either diel (24 h) or semi-diel (12 h) vertical migration of the particle when the period of the tide is semi-diurnal. The displacement is however much larger for the semi-diel (12 h) than for the diel (24 h) period and approaches infinity as the migration period approaches the semi-diurnal tidal period (12.42 h) (Fig. 13c). Hill (1991) also showed that for nonlinear forms of velocity shear, unidirectional transport is possible for multiple tidal migration periods.

In a study of the impact of advective processes on displacement of zooplankton biomass in a North Norwegian fjord system, Falkenhaug et al. (1995) showed that tidal displacement may have large consequences for the observed distribution of the zooplankton if organisms migrate through different layers during a 24-hour cycle. The current measurements, however, show that with a 24-hour migration cycle an organism will experience currents of opposite directions and thus may remain in the system.

Fig. 13. – a. Horizontal displacement of a vertically migrating organism; diel migration, semidiurnal tide; b. same as a. but semi-diel migration; c. Maximum horizontal displacement from the initial position \( x=0 \). (Redrawn from Hill, 1991).
Larval settlement in turbulent tidal flow

The diverse factors that affect recruitment of benthic invertebrates have been devoted attention in numerous papers which have greatly expanded the understanding of the diverse physical factors that affect the recruitment and the extent to which these factors may operate. Butman (1986) and others have shown by simple scaling arguments that most larvae disperse horizontally by currents essentially in a passive manner with only partial control of their vertical position. This means that hydrodynamic processes, i.e. vertical advection, turbulent mixing and shear and boundary layer processes, affect the intensities of the settlement.

To quantitively evaluate the relative influences of these processes upon settlement let us consider some of the results from Gross et al. (1992) who developed a time-dependent model of the tidal bottom boundary layer. They based their model on:

- the concentration equation:

\[
\frac{\partial C}{\partial t} + \frac{\partial (w_j C)}{\partial z} + \frac{\partial}{\partial z} \left[ A_v \frac{\partial C}{\partial z} \right] = 0
\]

- the momentum equations of u and v:

\[
\frac{\partial u}{\partial t} - f v = \frac{1}{\rho} \frac{\partial P}{\partial x} + \frac{\partial}{\partial z} \left[ A_v \frac{\partial u}{\partial z} \right]
\]

\[
\frac{\partial v}{\partial t} + f u = \frac{1}{\rho} \frac{\partial P}{\partial y} + \frac{\partial}{\partial z} \left[ A_v \frac{\partial v}{\partial z} \right]
\]

- the k-\( \epsilon \) (TKE-closure) turbulent kinetic energy equation:

\[
\frac{\partial k}{\partial t} = A_v \left[ \left( \frac{\partial u}{\partial z} \right)^2 + \left( \frac{\partial v}{\partial z} \right)^2 \right] + \frac{\partial}{\partial z} \left[ A_e \frac{\partial k}{\partial z} \right] - \epsilon
\]

where C = concentration of larvae, \( A_v \) = eddy diffusivity, \( A_e \) = turbulent energy diffusivity, \( w_j \) = larval fall velocity, both \( u,v \) = velocity components, \( P \) = pressure, \( \rho \) = density, and \( f \) = Coriolis parameter.

The solutions obtained with the TKE closure are shown in Fig. 14d. The suspended particle load simulated with the TKE closure is expected to be close to reality. However, in most existing models much simpler closures (eddy diffusive) are used.

To investigate how many solutions with simpler parameterization of the eddy diffusive parameter differ from the TKE closure, Gross et al. (1992) ran the model with three different eddy diffusivities introduced by Soulsby (1990).

Their model run with the three different eddy diffusivities are shown in Fig. 14a-c. The constant diffusivity gave poor results near the bed compared to simulation with TKE closure, but adequate in the outer regime while it was opposite for the linear diffusity. The best results were obtained with the mixed method while the constant coefficient gave very poor results as is seen in Fig. 14.

- Constant \( A_v(z,t) = C_d U_d(t) \)
- Linear \( A_v(z,t) = \kappa z [C_d U_d(t)]^{1/2} \)
- Mixed \( A_v(z,t) = \kappa z [C_d U_d(t)]^{1/2} \), \( z < Z_{bbl} \)
- Mixed \( A_v(z,t) = \kappa Z_{bbl} [C_d U_d(t)]^{1/2} \), \( z > Z_{bbl} \)

\( Z_{bbl} \) is the boundary layer thickness.

There are a large number of parameters required to specify a sinusoidally time dependent boundary
layer, larval suspension and settlement. An appropriate method to examine these parameters is by dimensional analysis to reveal fundamental nondimensional parameters to examine the behavior of the model. [For details see Gross et al. (1992)]. The momentum field can be fully nondimensionalized by specification of the following four variables:

\[
\begin{align*}
\text{u}_\text{max} & \quad \text{Maximum shear stress at the bed.} \\
T & \quad \text{Period of oscillation.} \\
h & \quad \text{Total depth.} \\
z_o & \quad \text{Roughness length scale of sea bed.}
\end{align*}
\]

while concentration field and bottom boundary condition are specified with:

\[
\begin{align*}
C_{\text{total}} & \quad \text{Total initial number of larvae in suspension per area.} \\
w_f & \quad \text{Fall velocity of particles.} \\
w_s & \quad \text{Settlement velocity (velocity out of the near bed region to the bed).}
\end{align*}
\]

Many different field conditions can now be examined by using these variables to form the following parameters:

\[
\begin{align*}
\frac{h}{z_o}, \frac{w_f}{u_{\text{max}}}, \frac{u_{\text{max}} T}{h}, \text{and} \frac{w_s}{w_f}
\end{align*}
\]

**Relative roughness** \( h/z_o \):

Kinetic energy closure requires a large Reynolds’ number in a flow layer (h) over a hydrodynamical rough bed layer with constant (z_o);

\[
[R_e/R_{\text{co}} = u_h/v/u_{\text{max}} v = h/z_o], \text{ h}/z_o \text{ is usually } > 10^4.
\]

**Boundary layer depth/Full depth** \( \delta_{bl}/h \):

This relation gives an indication of the height above the bed to which the turbulence generated near the bed will have an effect.

The height (\( \delta_{bl} \)) of an oscillating turbulent boundary layer depends on the turbulent strength and the period of oscillation:

\[
\delta_{bl} = \frac{\kappa u_{\text{max}} T}{2\pi} \text{ where } \kappa \text{ is a constant.}
\]

\((\kappa u_{\text{max}}): \text{ turbulence strength})\)

If \( \delta_{bl} < 1 \) then the depth of the boundary layer is less than the water column.

If \( \delta_{bl} > 1 \), turbulence is able to suspend material all the way to the surface.

**Rouse Number** \( w_f/\kappa u_{\text{max}} \):

This number gives a measure of the relative strength of downward flux due to fall velocity of an organism versus the upward turbulent suspension flux. A large Rouse number indicates that the larvae remain close to the bed.

**Settlement velocity/fall velocity** \( w_s/w_f \):

If the three mechanisms of larval movement: the advective fall flux \( w_f C \), the diffusive flux \( A_v \partial C/\partial z \) and the bed settlement flux \( w_s C \) are out of balance

![Image](Fig. 15. - Proportion of larvae \((C_{zc})\) below \( z_c \) (the distance in which a larvae is close enough to the bed to interact with the bed) as a function of phase of tide. There is a strong dependence of the near bottom concentration profile on \( w/\kappa u_{\text{max}} \) and a weak dependence on \( \delta_{bl}/h \) (from Gross et al., 1992).)
then the ratio of settlement flux \((w_s C)\) to either advective flux \((w_f C)\) or diffusive flux \((A_v \partial C/\partial z)\) becomes important. Either \(w_s/u_{\text{max}}\) or \(w_f/w_f\) may describe this ratio.

Larval settlement is also controlled hydrodynamically through the supply of larvae to the depth \(z_c\) where settlement may take place within “quiet” intervals between intense bursts of turbulence. Fig. 15 shows the dependence of the relative pool (relative to the total amount of larvae) of potential settlers \(C_{zc}\) for different values of turbulence levels and the relation fall velocities versus upward flux. Obviously there is a strong dependence of the near bottom concentration profile on \(w_f/\kappa u_{\text{max}}\) and a weak dependence on the boundary layer depth \((\delta_{bl}/h)\).

As is obvious from the discussion above, knowledge about the bottom shear stress is crucial to be able to estimate bottom settlement of larvae. The development of high-resolution current meters (acoustic doppler current meters) which has taken place in recent years has made it possible to measure bottom stress in the ocean and by such one is able to estimate the diffusive flux based on measurements.

The influence of advection on distribution of fish eggs and larvae

Another area which has been devoted attention for many decades is the link between horizontal advection and distribution of plankton, fish eggs and larvae. This has been studied in many ocean areas around the world. It is shown that there is a close relationship between the distribution of eggs and early stages of fish and advection processes. To illustrate this relation some results from one of the most intensively investigated areas, Georges Bank in the Gulf of Maine (Fig. 16), are presented. Physical and biological field investigations have been carried out for many decades in this area. The results, from numerous investigations carried out since the beginning of the twenties, may be summed up as follows (see Werner et al., 1993):

Biology:

- Haddock spawning takes place on Georges Bank, mostly over the Northeast Peak, in the period February-June with peak spawning in May-April (temperature dependent).
- Pelagic juveniles are centred over western Georges Bank and extending towards Great South Channel.
- Cod spawn throughout most of the year, peak from January to April, and are present on Georges Bank from November through June. Highest concentrations over the southern flank.
- Vertical distribution of cod and haddock eggs varies in space and time due to processes like buoyancy of the eggs and larvae, stratification and turbulence.
- Swimming capability increases as the larvae develop into pelagic juveniles.

Hydrodynamics:

- At any time the currents on Georges Bank may be divided into four main components: seasonally
varying mean current, low-frequency current fluctuations (wind events and passing eddies), tidal currents ($M_2$) and current fluctuations related to e.g. internal waves.

- Both seasonal variations in the mean local windstress, the large-scale coastal current, the persistent contribution from tidal rectification and from the density field, contribute to the seasonal intensification of the mean current pattern (gyre) on Georges Bank.
- The gyre strength on Georges Bank and the recirculation in Great South Channel are near their seasonal minima in March–April.
- There is weak stratification over the Bank in the winter except in the shelf-slope water.

Based on the information listed above, one is able to form a picture of which physical processes determine the observed distribution of eggs and larvae on the bank (Fig. 17a). However, to get knowledge about the relative importance of the tide, mean circulation and wind-driven circulation on the distribution on eggs and early life stages, a comprehensive and intensive field experiment is necessary. An alternative, and less costly method is to use 3-D models.

Werner et al. (1993) did a climatological study of the influence of mean advection and behavior on the distribution of cod and haddock early life stages on Georges Bank. In the study, using a harmonic finite element method, a 3-D non-linear shallow-water equations model with eddy viscosity closure in the vertical was applied. The forcing was the tides, windstress on the surface and a prescribed density field. For details see Lynch et al. (1992) and Lynch and Naimie (1993). Both passive particles (eggs) and active particles (larvae and juveniles, vertical as well as horizontal movements) were “released” in the model.

The simulations confirmed the influence of tidal currents, residual tidal currents, wind-driven currents and inflow from Scotian Shelf on the distribution of cod and haddock early life stages on George Bank (Fig. 17b). The observed distribution of cod and modelled combination of physical and biological processes gave convincing results as the observed and modelled distributions showed quali-
tative agreement. It was shown that an important part of the biological variations after spawning were determined by physical processes.

Also when looking at variability in eggs and larval distributions on the Bank related to high-frequency variations of the wind-field the observed (two seasons) and simulated distributions showed good agreement (Lough et al., 1994).

**Impact of man-made environmental changes on ecosystems**

Human activity may alter the physical environmental conditions for the living organisms in the ocean e.g. release of CO$_2$ and CFC-gasses to the atmosphere, pollution from industrial and agricultural areas supplied by major rivers and pollution which comes from discharges of cities and industrial complexes along the coast as well as shipping and hydroelectric power production which alters runoff patterns to marine ecosystems, and thus physical properties of the upper layer. This in turn affects numerous biological properties (e.g. Bugden et al., 1982; Kaartvedt and Svendsen, 1990a, 1990b, 1995; Kaartvedt et al., 1991).

To evaluate the impact of freshwater discharge on a fjord system in western Norway (Fig. 18), a comprehensive physical-biological field experiment was carried out. The study may be considered as a large “laboratory experiment” since the experiments were carried out before and after an agreed plan for running the powerplant during the experiments.

![Fig. 18](image_url)

**Fig. 18.** – a. Map of three of the Ryfylkefjords; b. Mean current (25-h sliding means) from four measuring depths at station H. (pos. values are up-fjord). The arrows indicate commencement and cessation of discharge. (From Kaartvedt and Svendsen, 1990a).

![Fig. 19](image_url)

**Fig. 19.** – Chlorophyll $a$ profiles from Hylsfjorden prior to (23 October) (open circles), and during discharge (27 October) (full circles). a. Station H1, b. Station H2, c. Station H3 and d. Station H4. (From Kaartvedt and Svendsen, 1990a).
During running of the powerplant the circulation pattern of the upper layer was totally changed (Fig. 18b). Most of the variability of the biomass distribution during all the experiments was explained by physical processes (Kaartvedt and Svendsen, 1990a; Kaartvedt and Svendsen, 1990b; Kaartvedt et al., 1991). An illustrative example is shown in Fig. 19. A comparison of the biomass distribution prior to and during discharge of freshwater from the powerplant showed large changes caused by the changes of the circulation pattern. As is obvious it was of vital importance for the interpretation of the biological data that the physical and biological data were sampled simultaneously since the change was directly related to the advection field.

CONCLUDING REMARKS

In this presentation only a few examples have been given of the many of biological processes in the ocean which mainly are governed by physical processes. It should be needless to mention that projects designed to study the biological processes in the examples shown must have physical investigation as a strongly integrated part of the projects. It is therefore an advantage that the marine biology community take the consequences of what we know today about the close relationship between biology and physical processes in the planning of the projects.

REFERENCES


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