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FORMATION OF MICROPATCHES BY ZOOPLANKTON-DRIVEN MICROTURBULENCES

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ABSTRACT

The distribution and behavior of tintinnids *Stenosemella nucula* have been measured in situ within a microlayer formed by 39 million individuals·liter^{-1} with an optical particle counting- and imaging-system. The parallel propulsions of the many animals add up and drive strong downwelling water currents. Preliminary results for swimming-speeds, -directions and organism-distributions are presented. Probably due to gyrotaxis (Kessler, 1985, 1986) or some unknown bio/physical processes the organisms are focused into their self-generated velocity profile. Similar phenomena have been described for very dense plankton cultures as "bioconvection" (Childress et al., 1975a, 1975b; Platt, 1961; Plesset and Winet, 1974; Plesset et al., 1975). The micropatches are 2–4 mm wide and 8–340 mm deep with organism concentrations up to 215 million tintinnids·liter^{-1}. The flows form small convection cells similar to Langmuir- or Benard-cells with distances between the patches of 8–30 mm. At the edge of the downwelling areas water velocity increases from near zero to 2–3 mm per s over a vertical distance of less than 1 mm resulting in considerable shear. Some ecological consequences of these microturbulences and microdistributions for predator-prey relationships and particle transports in eutrophic estuaries are discussed.

In the last decade extreme plankton blooms have been observed in the Baltic and Beltsea as a consequence of increased phosphorus and nitrogen loads. Striped structures in the cm-range are typically observed in some of these blooms. In this paper the ecological consequences of these structures on predator-prey relationships are studied, following the objectives of GLOBEC. The importance of turbulence and patchy distributions in the cm-range for the ecology and early life history of fish has been highlighted by Costello et al. (1990); Cushing (1983); Davis et al. (1991); Denman and Gargett (1983); Donaghay and Klos (1985); Gerritsen and Strickler (1977); Haury and Wiebe (1982); Haury et al. (1990); Houde (1982); Hunter and Thomas (1974); Lasker (1975, 1988); Mackas et al. (1985); Marrase' et al. (1990); Oiestad (1985); Okubo (1980); Osborn et al. (1990); Owen (1981); Platt and Denman (1978); Rothschild (1986, 1988); Rothschild and Osborn (1988); Steele (1978, 1980); Sundby and Fossum (1990); Vlymen (1977); Wroblewski (1984); Yamazaki and Osborn (1988); Yamazaki et al. (1991) and others. In this project the dynamics of extreme plankton aggregations in the feeding grounds of juvenile herring are investigated in situ with an optical particle counting-and imaging-system (Kils, 1989a, 1992).

MATERIAL AND METHODS

Optical and acoustical systems were deployed for behavioral studies of juvenile fish and zooplankton in an area known to be a major nursery ground for spring spawning herring in Kiel-Fjord (54.22.05 N, 11.09.05 E). In late summer, schools of juvenile herring (*Clupea harengus,* body lengths between 35 to 60 mm) migrate through this area into the open Baltic Sea. The visibility is generally very poor due to massive plankton blooms. The autonomous floating laboratory "ATOLL" (Kils, 1986) was anchored in this location, allowing for long time monitoring of the processes. Optical sensors mounted in front of underwater observation windows were used to measure the microdistribution and the behavior of predators and their prey in relation to ocean physics and biological gradients. In very calm weather conditions, dense aggregations of dinoflagellates, ciliates and tintinnids have been observed. This paper focuses on the striped aggregations of the tintinnids *Stenosemella nucula* that were observed to concentrate just below the sea surface and at the pycnocline. Our optical in situ particle counting- and imaging-system (Kils, 1989a) was focused into a thin (3–15 cm) layer of these tintinnids.

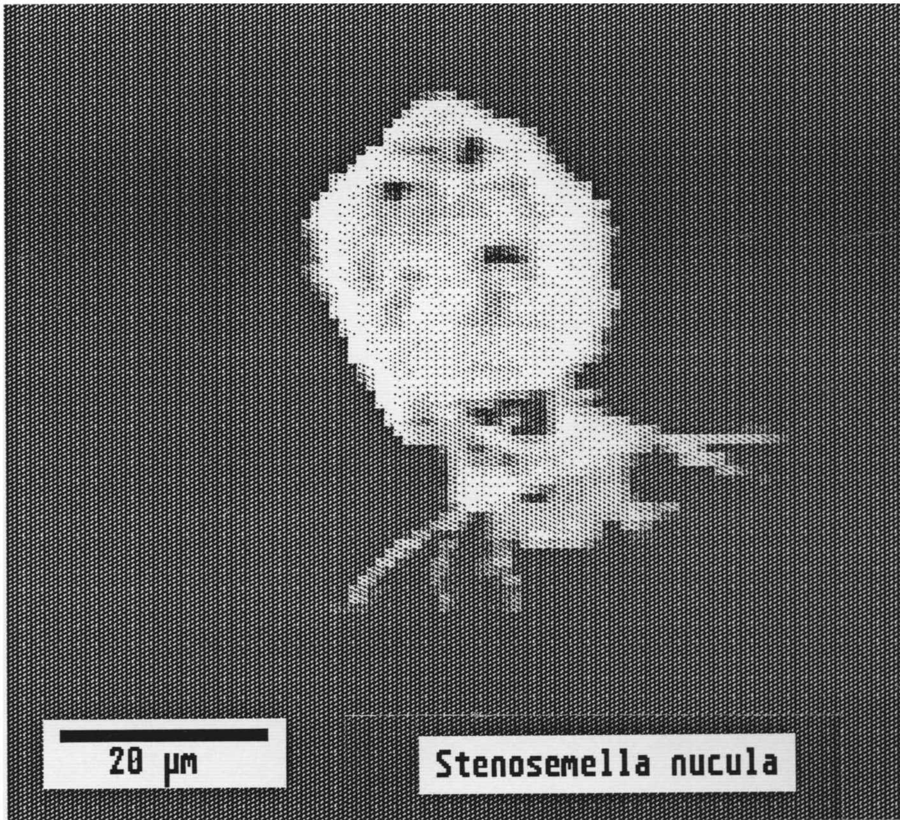

Figure 1. Digital image of the high magnification CCD-sensor allowing for raw taxonomic identification and sizing of the 30 µm organisms.

This system has sufficient resolution that an image (Fig. 1) of the digital readout of the high magnification CCD-sensor can be used for raw taxonomic identification and sizing of the 30 µm organisms. The microlayer was sampled additionally with a pump for exact taxonomy. A medium magnification CCD-sensor focused on the same thin layer (Figs. 2, 3) displayed each tintinnid as a small dot for distribution analysis. Images were scanned every 20 ms. The animations were processed with the software package dynIMAGE (Kils, 1992), filtering out system-vibrations and microturbulences in the dm-range, allowing for a compensated replay of the shifted animations and an evaluation of swimming-speeds, -directions, organism-concentrations, organism-microdistributions and microturbulences in the mm-range. For some measurements two perspex plates were swiveled vertically in front of the system to confine a 1.8 mm stratum allowing measurements of the same organisms over several minutes (Figs. 6, 7, 8). Additional information was gained from observations through the underwater-windows of the laboratory with binoculars (Kils, 1986) and by SCUBA-diving.

Results

Figure 4 shows the striped formation of the tintinnids. This figure is drawn from a photograph taken from above the water surface. The parallel stripes of high organism concentrations (painted black) have 10 to 30 mm spacings. These stripes sometimes join at several points, much as observed with stripes generated by Langmuir circulation. In the lower left quarter of the area, the pattern had been disturbed by stirring to uniform distribution 120 s before the picture was taken. Within this time the pattern nearly recovered.

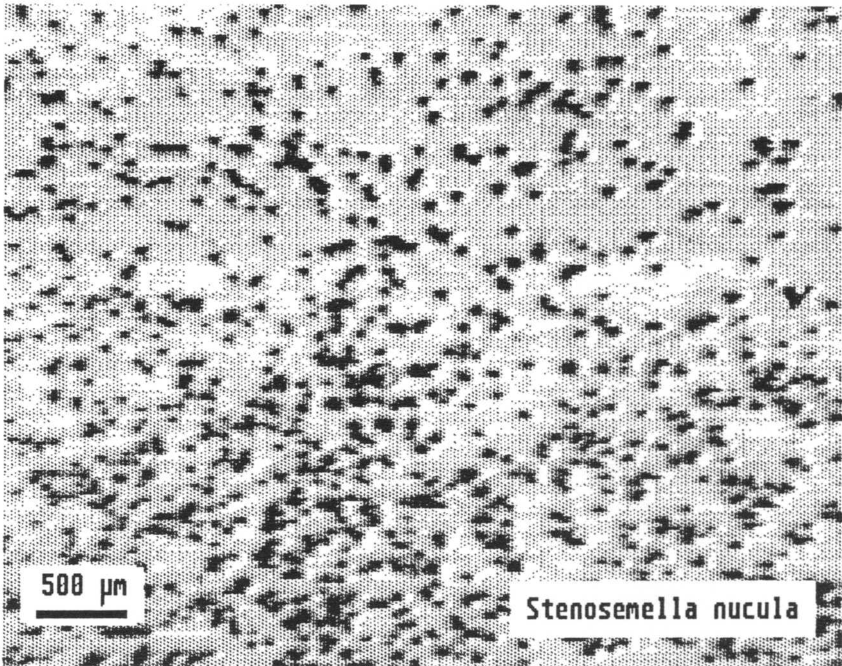

Figure 2. Horizontal view of the microlayer. Image from the medium magnification CCD-array, displaying each tintinnid as a small dot for distribution analysis.

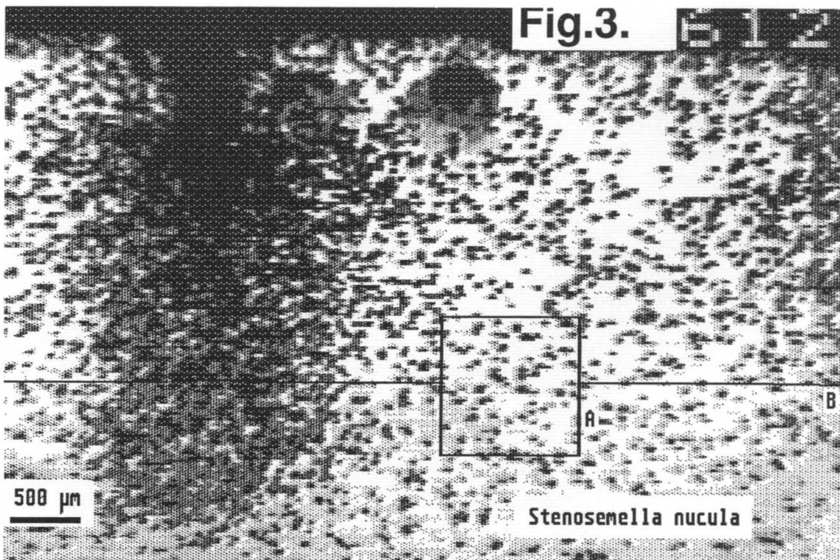

Figure 3. Horizontal view of the microlayer. Images from the medium magnification CCD-array, displaying each tintinnid as a small dot for distribution analysis. In the left part the beginning formation of a typical micropatch is imaged, at the right side the peripheral individuals of the next patch.

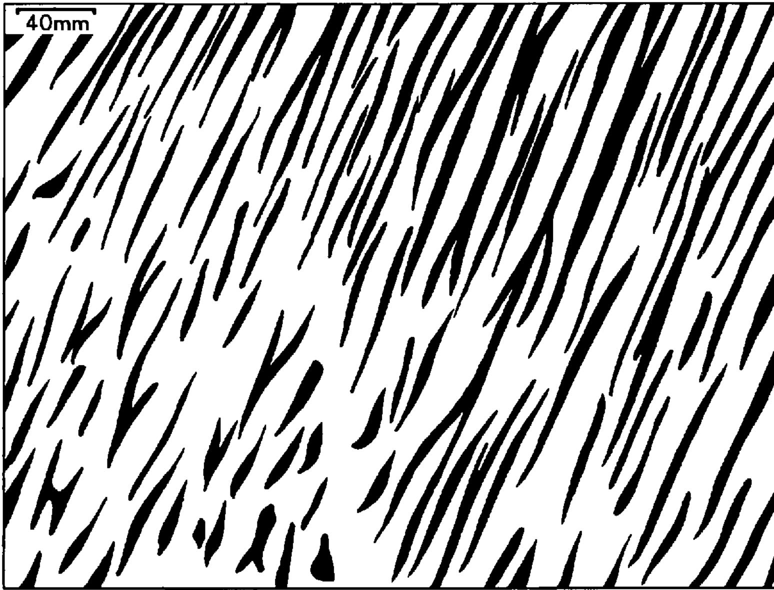

Figure 4. Striped formation of the tintinnids (drawn from a photograph taken of the water surface from above). Stripes of high organism concentrations are painted black.

Figures 2 and 3 give horizontal views of the microlayer. The distribution of the organisms is not random (Fig. 2) even when clear stripes are not obvious. The beginning of the formation of a typical micropatch can be seen in the left part of Figure 3, the peripheral individuals of the next patch can be seen at the right side of Figure 3.

Figure 5 gives the organism concentrations along a 25-mm-long horizontal

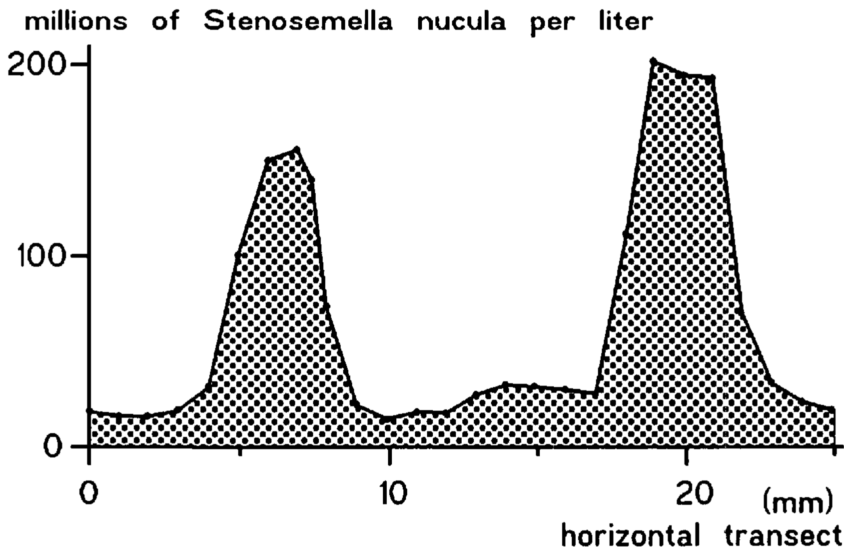

Figure 5. Organism concentrations along a 25 mm long horizontal transect across the centers of two micropatches: up to 200,000 individuals live in each milliliter.

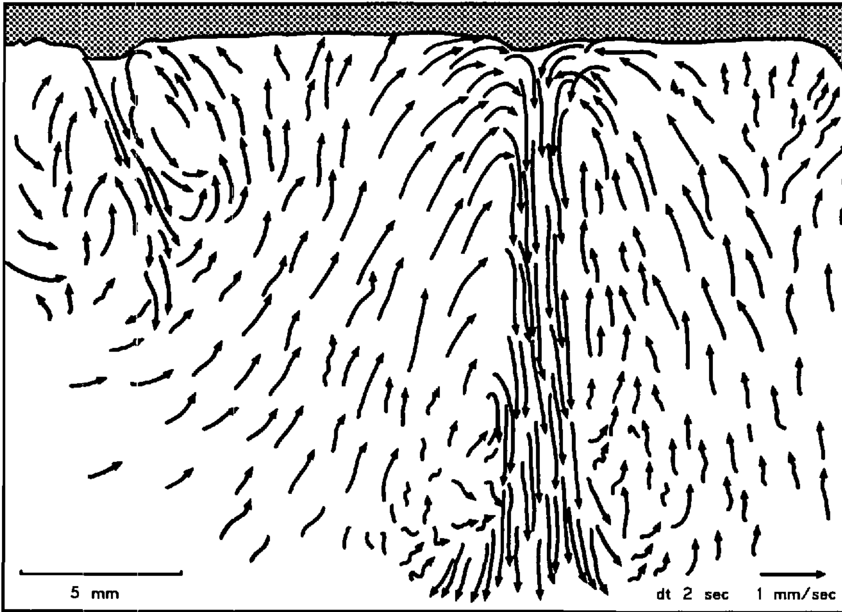

Figure 6. Tracks of tintinnids (horizontal view, mean density: 23 million individuals·liter^{-1}) plotted over a time-period of 2 s: in most of the areas the animals swim upwards at about 1 mm·s^{-1} but within a 2-mm-wide band the tintinnids are forced downwards at speeds of about 1.5 mm·s^{-1}. These animals still swim upwards at about 1 mm·s^{-1} against the downwelling of about 2.5 mm·s^{-1}. In the left part the formation of a new micropatch and convection cell can be observed (in the shaded area the organism concentrations were too high for an evaluation).

transect across the centers of two micropatches: up to 200,000 individuals live in each milliliter. The animals swim predominantly upwards, propelling the fluid downwards resulting in a water current running at speeds of 2–3 mm·s^{-1}.

To investigate the dynamics of a micropatch over several minutes, a 1.8-mm-thick sheet of the microlayer was confined between two perspex plates swiveled vertically in front of the optical system from the sides. In Figure 6 the tracks of tintinnids over 2 s are plotted: in most of the areas the animals swim upwards with about 1 mm·s^{-1} but within a 2-mm-wide band the tintinnids are forced downwards with a speed of about 1.5 mm·s^{-1}. These animals still swim upwards with about 1 mm·s^{-1} against the downwelling of about 2.5 mm·s^{-1}. In the left part of Figure 6 the formation of a new micropatch and convection cell can be observed.

In an additional experiment the confined microlayer was diluted with water from 20 cm below. At this lower concentration (1,900 individuals·ml^{-1}) no micropatches developed. In Figure 7 the tracks of the tintinnids are plotted over a time-period of 2 s: many animals swim upwards with a mean speed of 1.01 mm·s^{-1} (max. = 1.46, s = 0.18). Other animals move downwards with a mean speed of 0.26 mm·s^{-1} with very little variance (min. = 0.21, max. = 0.32, s = 0.026). These are predominantly sinking animals with no ciliary motion. It is not clear whether these animals were damaged by the experiment or singly passively sinking. Tintinnids are relatively heavy organisms.

Figure 8 shows a time series of the new formation of micropatches after artificially disrupting the structures by mixing up the confined microlayer (concentrations higher than approximately 50,000 organisms per ml are painted black):

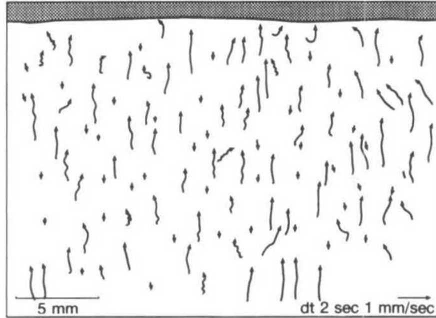

Figure 7. Tracks of the tintinnids (horizontal view, mean density: 1.9 million individuals·liter^{-1}) plotted over a time-period of 2 s: many animals swim upwards with a mean speed of 1.01 mm·s^{-1} (max. = 1.46, s = 0.18). Other animals move downwards with a mean speed of 0.26 mm·s^{-1} with very little variance (min. = 0.21, max. = 0.32, s = 0.026), (in the shaded area the organism concentrations were too high for an evaluation).

Due to the general upward swimming the animals concentrated below the water surface (Fig. 8, start). Twenty s later nuclei of many small patches developed, 10 mm deep with a spacing of 8 mm. Another 20 s later their depth increased to about 20 mm. At 80 s five 40-mm-deep patches can be observed whereas three others did not grow markedly. A typical process could be observed: within the next 40 s patches a and b join to form patch d at 120 s. In this patch the downwelling current is now driven by about twice as many animals, resulting in an accelerated water velocity forcing the tintinnids strongly downwards.

Measurements inside other microlayers of the flagellates *Prorocentrum minimum* (mean size 16 μm, swimming speed 0.190–0.320 mm·s^{-1}, mean densities 210,000–860,000 individuals·ml^{-1}, spacing between micropatches 8–45 mm), *Heterocapsa triquetra,* and another tintinnid showed similar results but still need to be analyzed.

Discussion

These preliminary evaluations of distribution and behavior from motile microorganisms display complex structures and dynamics in the dm- to mm-range inside dense plankton blooms recently observed in the Baltic Sea. The striped patterns are due to differences in abundance of several orders of magnitude over a distance of a centimeter. The micropatches coincide with convection cells running at downwelling speeds of 2–3 mm·s^{-1}. For dense cultures of motile algae and flagellates the formation of regular patterns has been described and termed "bioconvection" (Childress et al., 1975a, 1975b; Hill et al., 1988, 1989; Kessler, 1985, 1986; Loeffer and Mefferd, 1952; Pedley and Kessler, 1990; Plesset and Winet, 1974; Plesset et al., 1975; Platt, 1961). In the older theories these convection cells have been explained as thermal instabilities or density inversions. The thermal theory has been rejected by Platt (1961), citing Donelly (unpubl. data) who demonstrated bioconvection even under a very stable thermal gradient. The density theory has been rejected by Loeffer and Mefferd (1952), who demonstrated inhibition of the pattern formations when they blocked ciliary motion by Parathion.

Although the phenomenon is not fully understood, several recent theories are based on a physically determined taxis (Hill et al., 1988; Kessler, 1985, 1986;

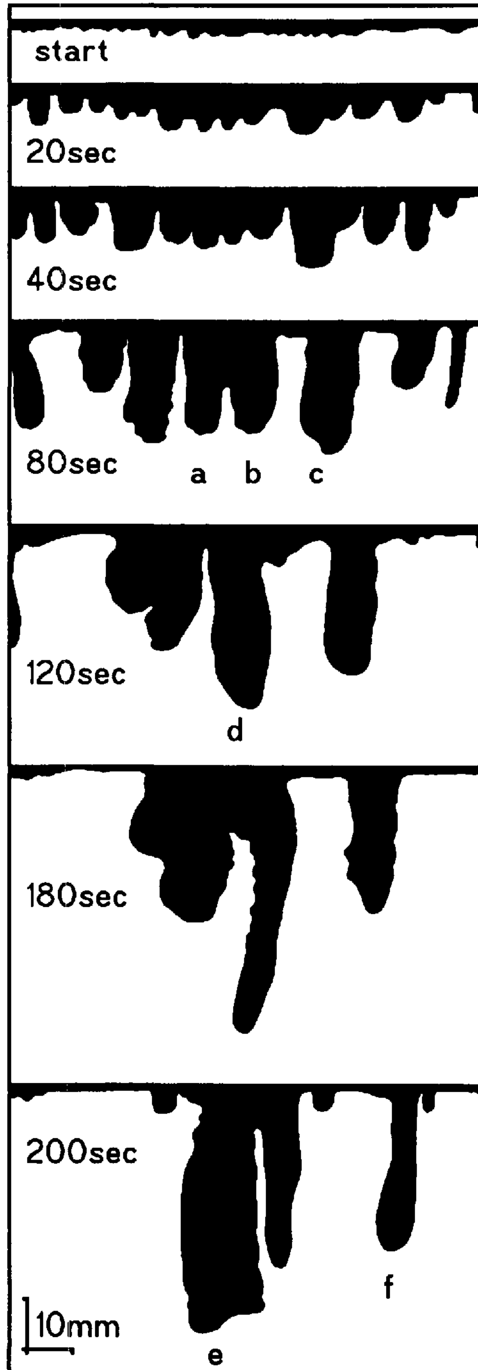

Figure 8. Time series of the formation of new micropatches after artificially mixing the confined microlayer (concentrations higher than approximately 50 million·liter^{-1} are painted black): Due to the general upward swimming the animals are concentrated just below the water surface (start). Twenty s later nuclei of many small patches developed, 10 mm deep with a spacing of 8 mm. Another 20 s later their depth increased to about 20 mm. At 80 s five 40-mm-deep patches can be observed whereas three others did not grow markedly. A typical process could be observed: within the next 40 s patches a and b join to form patch d at 120 s. In this patch the downwelling current is now driven by about twice as many animals, resulting in an accelerated water velocity forcing the tintinnids more strongly downwards.

Pedley and Kessler, 1990). "Gyrotaxis" guides swimming cells horizontally away from upwelling and towards downwelling regions of a fluid. The nucleus of downwelling, however, can arise from density instabilities caused by the many organisms with densities typically 3–8% above seawater (Fig. 2). Since many planktonic organisms show negative geotaxis and/or positive phototaxis, gyrotaxis guides them laterally into descending regions of the pelagic: motile organisms are focused into their self-generated velocity profile.

The preliminary in situ evaluations are similar to the data of the cited authors derived from cell cultures of the motile algal species *Chlamydomonas nivalis* and the flagellate *Euglena viridis*: cell sizes, gravity, swimming speeds and cell concentrations as well as the sizes of the resulting microaggregations and the downwelling velocities are similar. One marked difference is their horizontal distribution: in the culture vessels hexagonal patterns are described whereas in the sea the patterns are more in parallel stripes.

The difference might be due to small wind forces.

Although this and many other questions remain challenges for future cooperations between physical oceanographers and biologists, the phenomenon has some ecological implications: a) The extremely high organism concentrations in the downwelling areas provide excellent feeding conditions for particulate- and filter-feeders. An example of the utilization of the tintinnids by juvenile herrings is given in Kils (1989). b) In the areas between the patches the organism concentration is far below the average, with better visibility, less light attenuation and other effects than would be calculated from integrating net- or pump-samples. These stripes might be used as escape channels by organisms, for which contact with the bloom-species is detrimental. c) The relatively strong downwelling fingers should have some impact on the mixing of the surface layer: particles and organisms from the surface film can be forced downwards, and on very calm days heat O_2 and CO_2 from the stable surface layer could be transported several decimeters into the sea without wind forces. d) Organisms with low motility will be pushed down in the fingers and expelled out of the light flooded stratum. Such a sorting mechanism might serve as an additional explanation for the extreme predominance reported for some bloom-species. e) An interesting feature of the microflows is the high velocity-shear at the edge of the fingers, because the escape response of many pelagic animals is triggered by shear (Confer and Blades, 1975; Haury et al., 1980; Kerfoot et al., 1980; Singarajah, 1969, 1975, and Yen, 1988). Hwang et al. (this conf.) demonstrated that a turbulent disturbance of 0.84 $mm \cdot s^{-1}$ induced escape flights of *Centropages hamatus*. We observed copepods darting upon contacting a finger. Such repeated and senseless jumps should exhaust copepods after a while making them an easier prey for juvenile herrings (Kils, 1989a). f) The turbulent displacements of prey organisms in the convection cells should also have an effect on the contact rates of predator and prey as discussed by Gerritsen and Strickler (1977), Osborn et al. (1990), Rothschild (1986, 1988), Rothschild and Osborn (1988), Yamazaki and Osborn (1988) and Yamazaki et al. (1991).

Although the formations of micropatches by bioconvection are only very occasional events, they should have some ecological effects for coastal zones of the Baltic and enriched estuaries, possibly slowing down or buffering the biological collapse of nutrient stressed ecosystems.

More general knowledge about the interactions of very dense aggregations of motile animals with the fluid can also enhance our understanding of processes observed in aquacultural plants (Kils, 1989b) and in schools of *Euphausia superba*, a relatively heavy animal propelling much water downwards (Kils, 1981).

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