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Bimodal distribution patterns of motile phytoplankton in relation to physical processes and stratification (Gulf of Finland, Baltic Sea)

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ABSTRACT

The dynamics and vertical distribution patterns of chlorophyll *a* and motile phytoplankton species in relation to the vertical stratification and its spatial and temporal variations were analyzed on the basis of observational data collected in the Gulf of Finland in July 2010. Bimodal vertical distribution of phytoplankton characterized by a thick maximum in the upper 10 m layer and a thin maximum in the deeper part of the thermocline, where the chlorophyll *a* fluorescence values often exceeded those in the upper layer, was observed in the areas of locally weaker stratification at the mesoscale in the second half of July. We suggest that the observed bimodal distribution pattern was a result of the downward migration of phytoplankton through the thermocline at night and asynchronous upward movement of cells with a migration cycle longer than 24 h. The main species found in the sub-surface maxima were the dinoflagellates *Heterocapsa triquetra* and occasionally *Dinophysis acuminata*. Biomass of *H. triquetra* increased in the surface layer concurrently with the appearance of sub-surface biomass maxima under conditions of relatively high horizontal variability of vertical stratification at the mesoscale. It supports our suggestion that the mesoscale dynamics favors successful vertical migration of this species between the surface layer and deep nitrate reserves. Sub-surface maxima of phytoplankton biomass, as well as vertical migration, leading to selective transport of nutrients, have to be taken into account in the regional ecosystem models, both to forecast phytoplankton blooms and describe more precisely the seasonal dynamics of nutrients and phytoplankton primary production in the stratified estuaries.

1. Introduction

Vertical migration is widely acknowledged as an effective survival strategy for flagellated phytoplankton in stratified environments where the main resources—light and nutrients—are separated by physical gradients. In the case of shallow pycnoclines, cells are able to perform diel vertical migration aggregating near the sea surface during the day and in the pycnocline or near the seabed at night (Hall and Paerl, 2011; Sullivan et al., 2010). In estuaries where the euphotic depth and nitracline depth are well separated in summer, bimodal vertical distribution patterns have been often observed (Lips et al., 2010; Townsend et al., 2005).

It is suggested that the bimodal distribution of motile phytoplankton is a result of asynchronous vertical migration of cells between the euphotic upper layer and nutrient reserves below the pycnocline (Ralston et al., 2007). On the other hand, often, when bimodal distribution has been observed, the sub-surface maximum could be regarded as a thin phytoplankton layer according to the most recognized definition (Dekshenieks et al., 2001). Several physical processes, such as straining by shear, intrusion, and gyrotactic trapping, and biological processes including convergent swimming and *in situ* growth have been suggested as mechanisms of thin-layer formation and persistence (see an overview by Durham and Stocker, 2012). Recent studies in the field (Sullivan et al., 2010; Velo-Suarez et al., 2010) and in the mesocosms (Jephson et al., 2011) suggest that physical processes and stratification, as well as species-specific biological behavior, are crucial for the formation of biomass maxima below the pycnocline.

A number of studies have reported the occurrence of sub-surface or deep maxima of phytoplankton biomass in the Baltic Sea (Hällfors et al., 2011; Kononen et al., 2003; Gisselson et al., 2002). The main species forming such biomass maxima belong to dinoflagellates, *i.e.*, *Dinophysis acuminata* and *D. norvegica* Claparède and Lachmann 1859, found mostly in the Baltic Proper and the western Gulf of Finland (Hällfors et al., 2011), and *Heterocapsa triquetra* (Ehrenberg) Stein in the Gulf of Finland (Kononen et al., 2003). Kononen et al. (2003) suggested that the surface bloom of *H. triquetra* in the Gulf of Finland in summer 1998 was formed on the basis of a nitrate pool utilized by migrating cells below the thermocline. While the sub-surface biomass maxima and nocturnal, synchronous downward migration of *H. triquetra* was

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observed in July 2009 (Lips et al., 2011), the upward migration was not documented at the same site. It could be suggested that upward migration was asynchronous or took place at some other geographical locations.

The Gulf of Finland is a stratified estuary where nutrient-depleted surface waters are separated from the nutrient-rich deeper layers by the seasonal thermocline in summer. High values of kinetic energy of mesoscale fluctuations have been reported on the background of general cyclonic circulation (Laanemets et al., 2011; Alenius et al., 1998). In accordance with this, mesoscale patterns in horizontal distribution of phytoplankton in the surface layer of the Gulf of Finland are frequently observed, both in the field (Lips and Lips, 2010; Kononen et al., 1996) and using remote-sensing methods (Kahru et al., 2007). We hypothesize that the motile phytoplankton species benefit from the existing mesoscale circulation patterns in this stratified estuary. Since different species can form the sub-surface biomass maxima, the analysis of links between the mesoscale physical processes and phytoplankton dynamics should be species-specific and incorporate biological/ecological processes, such as migration behavior, mixotrophy, and the ability to utilize certain nutrient sources, such as organic nitrogen compounds in the thermocline or nitrate below it. Information on species forming sub-surface biomass maxima and their survival strategies is particularly important due to the fact that among them some are potentially toxic (Setälä et al., 2011) or can form harmful blooms (Lindholm and Nummelin, 1999).

The main aim of the present paper is to demonstrate the links between the physical processes and characteristics of bimodal vertical distribution of summer phytoplankton in the stratified Gulf of Finland. We focus our analysis on the dynamics and vertical distribution patterns of chlorophyll *a* and motile phytoplankton species in relation to the horizontal variability of vertical stratification at the mesoscale.

2. Material and methods

The data set analyzed in the present study was collected in summer 2010 in the Gulf of Finland, Baltic Sea (see map in Fig. 1A) by observations and sampling aboard a research vessel and a ferry traveling between Tallinn and Helsinki, autonomous measurements at a buoy station, and towed undulating-vehicle (Scanfish) surveys. Vertical profiles of temperature, salinity, and chlorophyll *a* (Chl *a*) were acquired weekly (or more frequently) at station AP5 from 30 June to 2 August using an OS320*plus* CTD probe (Idronaut S.r.l.) equipped with a Seapoint Chl *a* fluorometer. Water samples were collected with a vertical resolution of 5–10 m for analyses of inorganic nutrient (PO_4^{3-} and $NO_2^-+NO_3^-$) concentrations, Chl *a* content, and phytoplankton species composition and biomass.

The Ferrybox system (-4H- Jena Engineering GmbH) aboard the passenger ferry “Baltic Princess” (AS Tallink Grupp) recorded temperature, salinity, and Chl *a* fluorescence in the surface layer (water intake was approximately at 4 m depth) twice a day along the ferry route (Fig. 1A). Time resolution of measurements was 20 s corresponding approximately to a spatial resolution of 150 m. Water sampling upto 17 locations along the ferry route was conducted on 30 June, 5 July, 12 July, 18 July, 25 July, and 1 August. The water samples were analyzed for the same parameters as those collected by the research vessel.

The autonomous profiler (Idronaut S.r.l.; surface buoy designed by Flydog Solutions Ltd.) was deployed at station AP5 (Fig. 1A) from 30 June to 4 August. Vertical profiles of temperature, salinity, and Chl *a* fluorescence in the water layer from 2 to 45 m were acquired with a time resolution of 3 h and a vertical resolution of 10 cm. Measurements were conducted using an OS316*plus* CTD probe (Idronaut S.r.l.) equipped with a Seapoint Chl *a* fluorometer.

Surveys using a towed undulating vehicle (Scanfish) equipped with conductivity, temperature, pressure (Neil Brown Mark III), and Chl *a* fluorescence (Trios microFlu-chl-A, sampling rate 5 Hz) sensors were conducted to map the horizontal distribution of phytoplankton Chl *a* in the water column from 2 to 45 m. Data from the surveys on 20–21 July, 22 July, 26 July, 27 July, 30 July, and 2 August are used in the present analysis (see configuration of surveys in Fig. 1B). Before the surveys on 22 July and 2 August, the same cross-section was sampled at 13 stations (Fig. 1A) for CTD profiles and nutrient, Chl *a*, and phytoplankton species composition analyses from discrete samples. Vertical resolution of water sampling was 5 m, however, the sub-surface Chl *a* maxima were sampled at the depths of observed fluorescence peaks. All measurements were conducted mostly in the daytime with the exception of the polygon-like survey by Scanfish at night on 20–21 July.

The samples for nutrient analyses were deep-frozen after collection and analyzed at the on-shore laboratory using the automatic nutrient analyzer Lachat QuikChem 8500 Series 2 (Lachat Instruments, Hach Company). Nutrient analyses were carried out according to the recommendations of USEPA, ISO and

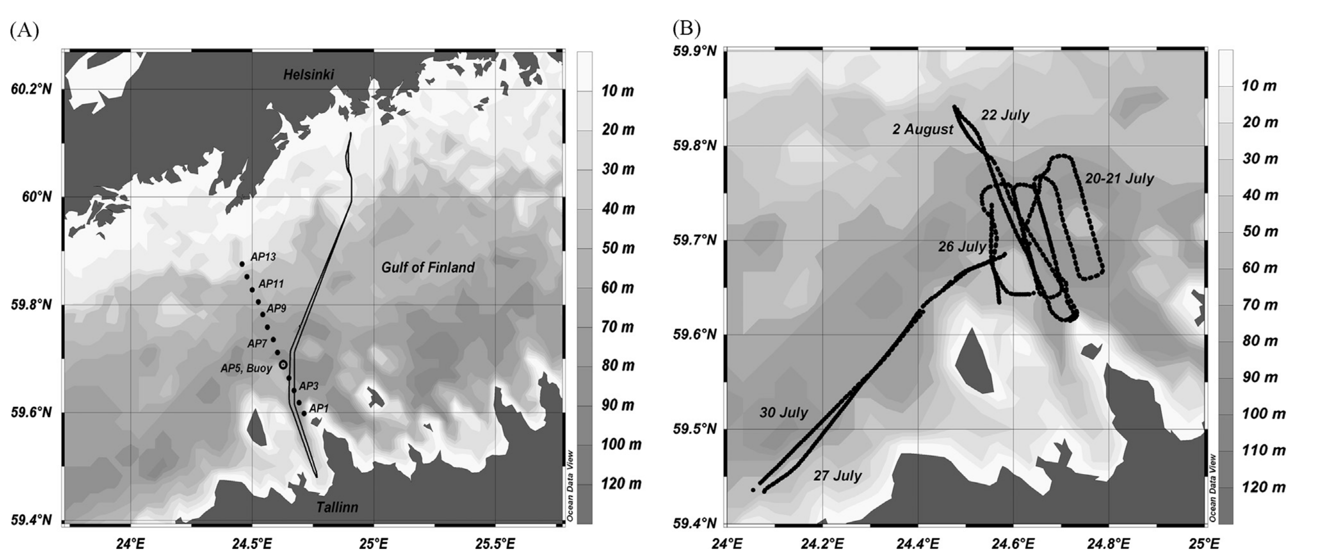

Fig. 1. Map of the study area where (A) locations of the sampling section AP1–AP13, buoy station (open circle), and ferry route Tallinn–Helsinki, and (B) towed undulating vehicle surveys are indicated.