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Vertical spatio-temporal patterns of phytoplankton due to migration behaviors in two shallow, microtidal estuaries: Influence on phytoplankton function and structure

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ABSTRACT

Vertical patterns of phytoplankton biomass driven by phytoflagellate migration constitute a natural, short-term process with potentially important impacts on estuarine primary production and community composition. Although often considered well-mixed, phytoflagellate vertical migration patterns have been observed in shallow estuaries. We investigated vertical migration patterns in two shallow estuaries to determine how often and under what environmental conditions vertical migration patterns occurred, and to understand the potential impacts of vertical migration on phytoplankton composition and productivity. Vertical migration patterns were determined from circumannual records of decimeter-scale, semihourly, vertical profiles of chlorophyll fluorescence in two shallow, microtidal estuaries, the New River Estuary and Neuse River Estuary, North Carolina, USA. Observed migration patterns were compared with coincident measures of temperature, salinity, light, turbidity, nutrients, vertical stratification, and wind speed. A simple light $\times$ biomass model was used to estimate the influence of vertical migration patterns on total water column primary production. Collectively, between two sites in each estuary, diel vertical migration (DVM) patterns were detected on about half of the days. A secondary migration pattern reflecting a midday descent was also observed and was attributed to avoidance of intense midday surface irradiance. The likelihood of detectable DVM patterns increased under warmer conditions and lower incident irradiance, and at two of the stations was lessened by elevated wind speeds or reduced stratification intensity. Even weak stratification may be sufficient to reduce vertical mixing to levels that allow effective depth regulation by directed swimming. Modeled depth-integrated primary production was increased modestly ($<10\%$) by observed migration patterns compared to a hypothetical vertically-homogenous biomass distribution. Access to optimal light levels and elevated bottom water dissolved inorganic nitrogen concentrations provides selective advantages that may explain phytoflagellate dominance in these estuaries, particularly during the warmer months, when production in surface waters of both systems is strongly N-limited.

1. Introduction

As the dominant primary producers in many estuaries, phytoplankton abundance and productivity play critical roles in determining water quality, fisheries yields, carbon and nutrient cycling (Paerl et al., 2014). Understanding the drivers of spatio-temporal patterns of phytoplankton is increasingly important for separating the effects of anthropogenic stressors (i.e. elevated nutrient and sediment loading) that are manageable at the watershed level from natural processes that are largely uncontrollable. It is becoming increasingly clear that natural externally-driven, short-term (hours to weeks) events and processes such as wind mixing events (Miller et al., 2006), floods and droughts (Paerl et al., 2014), heat waves and cold snaps (Buskey et al., 1998; Cloern et al., 2005) drive changes in estuarine phytoplankton communities by altering availability of nutrients and light, and changing the balance between population growth and losses due to grazing, settling, and advection from the system (Cloern and Jassby, 2010; Peierls et al., 2012). While the importance of these external short-term drivers on estuarine phytoplankton is well established, the importance of

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natural, internally-driven short-term processes has received comparatively less attention.

Vertical migration patterns represent a short-term process that is driven internally within the phytoplankton community. Synchronous diurnal vertical migration (DVM) is the most commonly documented migration pattern of phytoflagellates whereby cells swim to the well-lit surface waters during the day and migrate into deeper, often more nutrient rich, waters at night. Other vertical migration patterns include midday descents away from high near-surface irradiance (Passow, 1991; Ault, 2000; Hall and Paerl, 2011), and asynchronous diel vertical migrations whereby only a portion of a flagellate community migrates to deeper depths on any particular night (Ralston et al., 2007).

Changes in the depth distribution of phytoplankton coupled with the steep physical and chemical gradients in estuaries can result in dramatic increases in light and nutrient availability over short time (s to d) and spatial (cm to m) scales that can enhance intrinsic growth (Ault, 2000; Hall and Paerl, 2011; Peacock and Kudela, 2014). At the population level, coupling between the depth distribution of phytoplankton and vertical gradients of horizontal current velocities may decrease advective losses (Anderson and Stolzenbach, 1985; Crawford and Purdie, 1992). Additionally, mismatches in the vertical location of phytoplankton and zooplankton patches can decrease grazing losses (Jones, 1991; Salonen and Rosenberg, 2000). Since phytoplankton taxa vary in their ability to regulate their depth, the vertical physical and chemical gradients that confer advantages on species more adept at depth regulation are important determinants of community structure (Margalef, 1978; Ganf and Oliver, 1982; Fogg, 1991) and may play an important role in determining the spatio-temporal patterning of estuarine phytoplankton assemblages.

Water quality and ecosystem simulation models that are used to explore and predict impacts of human and natural drivers on estuaries rarely include vertical migration behaviors, even those that simultaneously model flagellated and non-flagellated phytoplankton functional groups (e.g. Cerco and Cole, 1993; Heironymous and Bowen, 2006). Is this effort to avoid overly complex models justified? Or, does it disregard an advantageous behavioral adaptation that is expressed with a high enough frequency to play an important role in shaping spatio-temporal patterns of estuarine phytoplankton assemblages and their impacts on production and biogeochemical cycling?

We do not, therefore, always know until we have had a great deal of empirical experience, whether a given example of structure is very extraordinary, or a more trivial expression of something which we may learn to expect all the time (Hutchinson, 1953).

To our knowledge, there have been no studies that document how often the resultant temporal/vertical structuring of phytoplankton biomass by vertical migrations occurs in estuarine systems. The simple presence of flagellate species with documented migration behaviors does not confirm that the behaviors are expressed. Under some physiological (e.g. strong nutrient deficiency) or environmental conditions (e.g. low temperatures/steep salinity gradients), phytoflagellates may or may not undergo vertical migrations (Heaney and Eppley, 1981; Tyler and Seliger, 1981; Doblin et al., 2006; Jephson and Carlsson, 2009). The intensity and duration of intermittent turbulence also determines whether phytoflagellate swimming is effective in producing vertical movements of flagellate patches against the homogenizing effect of large turbulent eddies (Karp-Boss et al., 2000). Small-scale shear associated with turbulence can also impair migration at the cellular level through physical damage to flagella (Thomas and Gibson, 1990). Shallow estuaries are highly susceptible to intermittent turbulent mixing from tidal and wind-driven shear, and the lack of persistent or seasonal stratification often leads to their characterization as being well-mixed (Mallin and Paerl, 1992; Phlips et al., 2012). If median (i.e. most of the time) rates of vertical mixing in shallow estuaries are strong enough, vertical migration patterns may be a rather infrequent occurrence.

This study examined four circumannual records of semi-hourly, decimeter-scale vertical profiles of chlorophyll in vivo fluorescence (IVF), salinity, temperature, and turbidity collected by autonomous vertical profiling (AVP) buoys at two sites in each of two shallow, microtidal estuaries, the Neuse River Estuary (NRE) and New River Estuary (NewRE), North Carolina, USA. Light and nutrient availability were monitored at each site to place observed phytoplankton depth distributions in the context of vertical gradients of growth limiting resources. The goals were to: 1) determine the frequency of occurrence of DVM populations, 2) determine the environmental conditions associated with DVM occurrence and the influence of DVM on access to light and nutrients, and 3) identify ecosystem-level ramifications of vertical migration on phytoplankton biomass, productivity, and composition.

2. Methods

2.1. Study sites

Both the NewRE and NRE (Fig. 1) are shallow, microtidal estuaries with average depths and tidal amplitudes of ~1.5 m and 0.25 m in the NewRE (Ensign et al., 2004) and ~3.5 and <0.1 m in the NRE (Luettich et al., 2000). Salinity ranges from oligohaline to polyhaline in the NewRE and oligohaline to mesohaline in the NRE (Luettich et al., 2000; Hall et al., 2013). Residence times for both estuaries are normally a few months but are longer during low river flows, and can be less than a week under very high flow conditions (Peierls et al., 2012). Both estuaries receive excessive anthropogenic nutrient loads and exhibit classic symptoms of eutrophication, including bottom water hypoxia, and harmful algal blooms comprised primarily of flagellated dinoflagellates and raphidophytes (Paerl et al., 1998; Mallin el. 2005; Hall et al., 2013). Phytoplankton production of these estuaries is predominantly limited by nitrogen availability, but light availability is also an important factor (Paerl et al., 2004; Mallin et al., 2005). Suspended sediment concentrations in both estuaries are moderate but freshwater inputs contain high chromophoric dissolved organic matter (CDOM) levels (Woodruff et al., 1999; Anderson et al., 2013) that create high background light attenuation even in the absence of phytoplankton absorption.

2.2. Autonomous vertical profilers

AVPs were deployed in the NewRE at Morgan Bay (34° 42.197′ N, −77° 24.228′ W) and Stones Bay (34° 35.758′ N, −77° 24.690′ W) (Fig. 1) on 14 and 12 June 2008, respectively, and the data record analyzed ended on 31 September 2012. Deployments in the NRE were conducted at NRE120 (34° 56.933′ N, −76° 48.912′ W) from 19 November 2001–26 December 2002, and at NRE180 (35° 3.848′ N, −76° 31.560′ W) from 25 May 2003–26 August 2004. Average depths at Morgan Bay, Stones Bay, NRE120, and NRE180 deployment sites were 3.0, 2.5, 4.6, and 6.9 m, respectively. The AVPs consisted of a moored floating platform housing a computer controlled winch mechanism (Reynolds-Fleming et al., 2002) that casted a YSI 6600 sonde (Yellow Springs Inc, Yellow Springs, Ohio). Profiles of temperature, salinity, turbidity, pH, dissolved oxygen and IVF of chlorophyll were produced every 30 min. The YSI 6025 IVF probe (model 6025) utilizes a 470 nm light emitting diode excitation source and 650–700 nm band pass emission filter (YSI 6-Series User's Manual). Approximately ten percent of the water depth at the surface and bottom was not measured by the AVPs. Winch speed and sampling frequency of the YSI 6600 data sondes were set to achieve a nominal