



# Assessing spatial and temporal variability of phytoplankton communities' composition in the Iroise Sea ecosystem (Brittany, France): A 3D modeling approach

## Part 2: Linking summer mesoscale distribution of phenotypic diversity to hydrodynamism



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### ABSTRACT

Tidal front ecosystems are especially dynamic environments usually characterized by high phytoplankton biomass and high primary production. However, the description of functional microbial diversity occurring in these regions remains only partially documented. In this article, we use a numerical model, simulating a large number of phytoplankton phenotypes to explore the three-dimensional spatial patterns of phytoplankton abundance and diversity in the Iroise Sea (western Brittany). Our results suggest that, in boreal summer, a seasonally marked tidal front shapes the phytoplankton species richness. A diversity maximum is found in the surface mixed layer located slightly west of the tidal front (i.e., not strictly co-localized with high biomass concentrations) which separates tidally mixed from stratified waters. Differences in phenotypic composition between sub-regions with distinct hydrodynamic regimes (defined by vertical mixing, nutrients gradients and light penetration) are discussed. Local growth and/or physical transport of phytoplankton phenotypes are shown to explain our simulated diversity distribution. We find that a large fraction (64%) of phenotypes present during the considered period of September are ubiquitous, found in the frontal area and on both sides of the front (i.e., over the full simulated domain). The frontal area does not exhibit significant differences between its community composition and that of either the well-mixed region or an offshore Deep Chlorophyll Maximum (DCM). Only three phenotypes (out of 77) specifically grow locally and are found at substantial concentration only in the surface diversity maximum. Thus, this diversity maximum is composed of a combination of ubiquitous phenotypes with specific picoplankton deriving from offshore, stratified waters (including specific phenotypes from both the surface and the DCM) and imported through physical transport, completed by a few local phenotypes. These results are discussed in light of the three-dimensional general circulation at frontal interfaces. Processes identified by this study are likely to be common in tidal front environments and may be generalized to other shallow, tidally mixed environments worldwide.

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### 1. Introduction

Marine phytoplankton play a key role as the first link in ocean food webs, producing almost 50% of the Earth's annual net primary production (Field et al., 1998). In every location of the ocean, a large number of photoautotrophic species, both prokaryotic and eukaryotic (Falkowski et al., 2004), with very diverse genetic, taxonomic or

functional characteristics generally coexists and contributes to biological production at higher trophic levels. The maintenance of high biological diversity is crucial to ensure resilience of ecosystem functioning (Ptcnik et al., 2008) as it allows complementarity between species or taxa to efficiently access heterogeneously distributed resources (Chisholm, 1992). Coexistence between phenotypes having various physiological and functional traits is enabled by several top-down or bottom-up complementary mechanisms. An example of top-down control is the regulation of primary producers' diversity by herbivorous consumers (i.e., zooplankton) that adjust their predation to the most

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abundant prey (e.g., through prey selectivity as described in Chase et al., 2002 and Hillebrand et al., 2007). On the other hand, bottom-up control can occur through ecological processes of adaptation (i.e. selection of optimal traits within evolutionary mutational changes), acclimation (i.e. phenotypic plasticity) enabling species locally adapted to environmental conditions to thrive and exclusive competition. As long as the residence time of water masses is sufficiently long (i.e., quasi steady state), this last process occurs, benefiting species with the highest fitness with a negative impact on the diversity. Indeed, following resource competition theory (Tilman, 1977, 1982), species with the lowest positive equilibrium resource concentration  $R^*$  (which measures the fitness of each phenotypes) outcompete other, less locally adapted organisms over time. This process of natural selection (bottom up control) could lead to diversity decline. However, high variability in environmental conditions at timescales similar to phytoplankton ecological rates can prevent complete exclusion and contributes to the maintenance of high diversity levels (Hutchinson, 1961; Sommer, 1984; Huston, 1979; Huisman and Weissing, 2001; Scheffer et al., 2003).

Local ecological processes alone are not sufficient to explain observed diversity patterns in the ocean. Indeed, apart from modulating the background environmental conditions, physical processes also noticeably gather phytoplankton types from different regions through advective transport by ocean currents combined with mixing that yields dispersion. The contemporaneous disequilibrium framework (Richerson et al., 1970) suggests that dispersal in a dynamic ocean contributes to maintain low fitness phenotypes in significant proportion by preventing the system from reaching a stable equilibrium. Indeed, as described by MacArthur and Wilson (1967), passive movements of species by physical transport associated with mixing have the potential to significantly affect qualitative and quantitative measures of local diversity by combining properties from different regions.

According to the neutral theory of biodiversity (Hubbell, 2001), the fate of species that are considered to be equivalent in terms of fitness is locally governed by stochastic processes (ecological drift) rather than determined by environmental traits selection. In contrast with niche segregation theory and resource competition, the observed diversity patterns would therefore be primarily explained by replenishment or discharge of local species pool through physical dynamics. Processes of local growth, exclusive competition and physical dispersal all shape the ocean diversity landscape and interact such that their individual impact depends on their relative timescale (Clayton et al., 2013).

At the global scale, marine microbial diversity has been explored through several field studies (Hillebrand, 2004; Irigoien et al., 2004; Pommier et al., 2007; Fuhrman et al., 2008) and modeling efforts (Barton et al., 2010). Species richness varies with latitude, generally decreasing from tropics to poles (corresponding to a low to high environmental variability). Also, it has been shown that dynamical transport contributes to higher local diversity ( $\alpha$ ) by decreasing the differences between distinct oceanic regions in terms of phytoplankton community composition (Clayton et al., 2013; Levy et al., 2014). Thus, local and regional diversity patterns are strongly influenced by large-scale diversity (Ricklefs, 1987). Transport over about a hundred kilometers is sufficient and acts sufficiently rapidly to significantly shape the diversity of planktonic ecosystems at local scales (Adjou et al., 2012).

At a more regional scale, physical dynamics induced by the presence of time-evolving mesoscale (10–100 km) structures with a lifetime of the same order of magnitude as phytoplankton generation timescales (D'Ovidio et al., 2010) also impact the regional diversity landscape in many distinct ways. Indeed, besides passive stirring of organisms between physical regimes, these structures may create ecological niches through variability in nutrient supply (Sedigh Marvasti et al., 2016), resulting in heterogeneously distributed primary producers' abundance, total chlorophyll (Gaube et al., 2014) and diversity patterns (McGillcuddy and Dennis, 2016). Uptakes rates, primary production (Levy et al., 2001; Rivière and Pondaven, 2006) and carbon export (Sharples, 2008) are likewise affected by mesoscale eddies and fronts.

Because the lifetime of eddies or vortices is longer than a few days, water masses in their interiors remain isolated and could act as shelters for less-fit species (Bracco et al., 2000; Perruche et al., 2010) whereas their edges and other frontal interfaces are generally more diverse than surrounding areas (Lévy et al., 2015) for two complementary reasons. High biomass associated with widely diversified plankton communities at frontal interfaces are then explained by (i) the encounter of water masses from both sides of the front (Perruche et al., 2010) potentially increasing the number of different species coexisting locally at the interface and (ii) the local growth of opportunistic fast growing phenotypes which may be enabled by vertical mixing and a net upward nutrient flux into the euphotic layer (Levin and Paine, 1974; Claustre et al., 1994; Barton et al., 2014).

However, the relative importance of these two complementary mechanisms (passive transport and local growth) on high diversity at fronts has not been effectively tested. Here, we explore how much phenotypic diversity in phytoplankton can be sustained by lateral and vertical advection and/or mixing relative to local growth in a highly dynamic tidal front environment with heterogeneous growth conditions including both spatial and temporal variability. To answer this question, we use a coupled physical/biogeochemical model including a large number of phytoplankton phenotypes which are differentiated by their optimal growth conditions (temperature, nutrient and light) and therefore compete for resources while they are consumed by zooplankton grazers and carried by currents.

This modeling setup is applied to the Ushant Front ecosystem of the Iroise Sea. The Ushant front is characterized by a sharp horizontal temperature gradient of  $2\text{ }^{\circ}\text{C}\cdot\text{km}^{-1}$  (Mariette, 1983) associated with high chlorophyll concentration during summer, from May to October (Le Boyer et al., 2009). Its position, located roughly where the  $15\text{ }^{\circ}\text{C}$  surface temperature isotherm intersects the surface (Fig. 1), oscillates with different time frequencies, varying from seasonal to bi-weekly and semi-diurnal periods according to tidal fluctuations and annual forcing variations. Observed high phytoplankton biomass in the vicinity of the front location has been shown to be related to a local increase of inorganic nutrients (Savidge, 1976). In this study, we use the model to investigate underlying processes contributing to biomass and phenotypic diversity patterns at the front. We specifically examine interactions between phenotypes competing for light and macronutrients in this very dynamic frontal environment. We aim to quantify the relative roles of local ecological processes and physical transport in shaping the diversity of this frontal ecosystem.

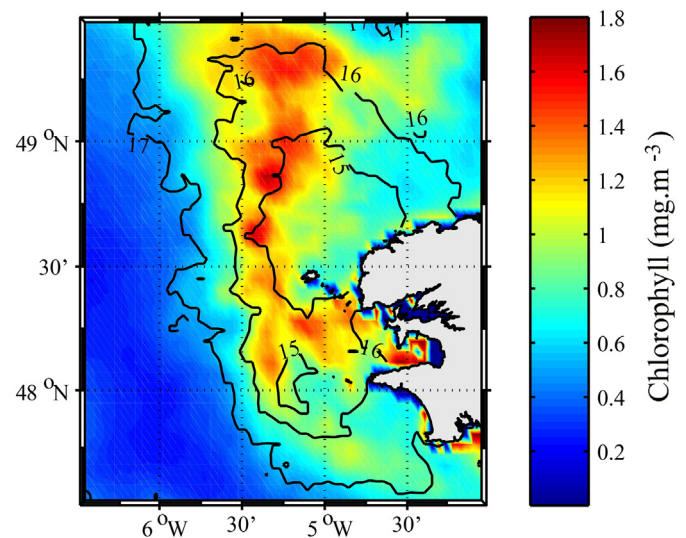


Fig. 1. Surface chlorophyll in September 2007, computed from SeaWiFS satellite observations, following Gohin et al. (2002). Black contour line represents Sea Surface Temperature from MODIS.

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