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Drivers of the winter–spring phytoplankton bloom in a pristine NW Mediterranean site, the Bay of Calvi (Corsica): A long-term study (1979–2011)

Anne Goffart[a,*], Jean-Henri Hecq[a], Louis Legendre[b,c]

[a] University of Liège, Laboratory of Oceanology, MARE Centre, B6c, 15 allée du 6 août, 4000 Liège Sart-Tilman, Belgium
[b] Sorbonne Universités, UPMC Univ. Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-Mer, France
[c] CNRS, UMR 7093, LOV, Observatoire océanologique, 06230 Villefranche-sur-Mer, France

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ABSTRACT

This work is based on a long time series of data collected in the well-preserved Bay of Calvi (Corsica island, Ligurian Sea, NW Mediterranean) between 1979 and 2011, which include physical characteristics (31 years), chlorophyll a (chl *a*, 15 years), and inorganic nutrients (13 years). Because samples were collected at relatively high frequencies, which ranged from daily to biweekly during the winter–spring period, it was possible to (1) evidence the key role of two interacting physical variables, i.e. water temperature and wind intensity, on nutrient replenishment and phytoplankton dynamics during the winter–spring period, (2) determine critical values of physical factors that explained interannual variability in the replenishment of surface nutrients and the winter–spring phytoplankton bloom, and (3) identify previously unrecognised characteristics of the planktonic ecosystem. Over the >30 year observation period, the main driver of nutrient replenishment and phytoplankton (chl *a*) development was the number of wind events (mean daily wind speed >5 m s^{-1}) during the cold-water period (subsurface water ⩽13.5 °C). According to winter intensity, there were strong differences in both the duration and intensity of nutrient fertilisation and phytoplankton blooms (chl *a*). The trophic character of the Bay of Calvi changed according to years, and ranged from very oligotrophic (i.e. subtropical regime, characterised by low seasonal variability) to mesotrophic (i.e. temperate regime, with a well-marked increase in nutrient concentrations and chl *a* during the winter–spring period) during mild and moderate winters, respectively. A third regime occurred during severe winters characterised by specific wind conditions (i.e. high frequency of northeasterly winds), when Mediterranean "high nutrient – low chlorophyll" conditions occurred as a result of enhanced crossshore exchanges and associated offshore export of the nutrient-rich water. There was no long-term trend (e.g. climatic) in either nutrient replenishment or the winter–spring phytoplankton bloom between 1979 and 2011, but both nutrients and chl *a* reflected interannual and decadal changes in winter intensity.

1. Introduction

Phytoplankton blooms are events of rapid production and accumulation of biomass, i.e. transient departures from the usual quasi-equilibrium, when primary production temporarily exceeds grazing and sinking losses and transport (Paerl, 1988; Legendre, 1990; Cloern, 1996). In temperate zones, exceptionally high concentrations of phytoplankton develop during relatively short periods of the year, especially at the end of winter and during spring. Annually recurrent blooms imply that the ecosystem recreates, over the autumn and winter, the conditions necessary for a buildup of biomass, showing that the winter–spring bloom is not an isolated event, but a feature of the annual cycle (Evans and Parslow, 1985; Behrenfeld, 2010).

Favourable conditions for phytoplankton growth occur when high concentrations of deep nutrients have been injected to the photic layer by vertical water exchanges, and irradiance is high enough for photosynthesis to exceed respiration (e.g. Mann and Lazier, 1996; D'Ortenzio and Prieur, 2012). The factors that cause nutrient replenishment of the upper layer by deep vertical mixing include processes that increase surface water density by cooling or evaporation, those processes being largely driven by cold air temperature and dry wind stirring (Williams and Follows, 2003; Salat et al., 2010). Mixing is particularly strong in the surface layer,

* Corresponding author. Tel.: +32 43665076, +33 683713223.
E-mail addresses: A.Goffart@ulg.ac.be (A. Goffart), JH.Hecq@ulg.ac.be (J.-H. Hecq), legendre@obs-vlfr.fr (L. Legendre).

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where there are continuous exchanges of energy with the atmosphere (D'Ortenzio and Prieur, 2012).

In the Western Mediterranean Sea, the occurrence of the winter–spring phytoplankton bloom is one of the most characteristic features of planktonic ecosystems, and a second, less intense peak in phytoplankton biomass develops in some areas in late summer or autumn (Estrada et al., 1985; Zingone et al., 1995; Licandro et al., 2006). There is high variability in the timing of the blooms over the basin (e.g. Bosc et al., 2004; D'Ortenzio and Ribera d'Alcalà, 2009; Bernardello et al., 2012). In offsfore waters, the winter–spring bloom occurs between the end of February and the beginning of May (e.g. Morel and André, 1991; Marty and Chiavérini, 2010; Siokou-Frangou et al., 2010). In coastal areas, the most common pattern is the occurrence of a phytoplankton bloom in February–March (Herrera and Margalef, 1961; Estrada et al., 1985; Charles et al., 2005), but variability amongst regions and years is higher than in offshore waters. For example, peak values in chlorophyll *a* (chl *a*) have been reported to occur between January in Banuyls-sur-Mer (Gulf of Lion; Neveux et al., 1975) and Blanes Bay (NE Spain; Duarte et al., 1999) and in May in the Gulf of Naples (Thyrrhenian Sea, Ribera d'Alcalà et al., 2004).

In the offshore waters and coastal areas of the Mediterranean Sea, the characteristic winter–spring bloom has been reported to develop in the upper water column when surface heating increases water column stability and thus causes the beginning of summer stratification (e.g. Estrada, 1996; Duarte et al., 1999). In these waters during the following stratified period, chl *a* concentration in the upper layer is very low, and a well-marked deep chl *a* maximum develops at the depth of the nitracline (Estrada et al., 1985; Marty et al., 2002).

In offshore Mediterranean waters, the strong interplay between physical processes acting on the distribution of nutrients and phytoplankton phenology has been studied at different temporal and spatial scales using both field (e.g. Andersen and Prieur, 2000; Vidussi et al., 2000; Marty et al., 2002) and modelling (e.g. Crise et al., 1999; Lazzari et al., 2012; Lavigne et al., 2013) approaches. Overall, these studies have indicated that the wind is the most relevant factor that influences the annual buildup of phytoplankton biomass (e.g. D'Ortenzio and Ribera d'Alcalà, 2009; Siokou-Frangou et al., 2010; Olita et al., 2011). However, no Mediterranean data series has had both the time resolution and duration to identify unambiguously the processes that control the interannual variability of phytoplankton blooms and quantify these processes.

Contrary to the offshore waters, few studies only have addressed the long-term responses of phytoplankton to physical forcing in Mediterranean coastal areas. The few available nutrient and phytoplankton time series concern highly urbanised areas, where long-term variability reflects the combined effects of climate and anthropogenic forcing, e.g. land-derived nutrients delivered to coastal waters by river discharges (Bernardi Aubry et al., 2004; Mozetič et al., 2010; Arin et al., 2013), fertiliser runoff and industrial effluents (Ninčević Gladan et al., 2010), urban runoff from very densely populated regions (Ribera d'Alcalà et al., 2004; Zingone et al., 2010), and aquaculture (Sara et al., 2011). The studies based on these time series could not distinguish the responses of phytoplankton to physical forcing from those induced by multiple human disturbances. To our knowledge, the only investigations in a coastal Mediterranean area free from local anthropogenic pressure have been conducted in the Bay of Calvi (Corsica, Northwestern Mediterranean; Goffart, 1992; Goffart et al., 2002; Skliris et al., 2001a).

In the present study, we use a long-term time series of observations made in the Bay of Calvi between 1979 and 2011, to investigate the effects of key natural drivers on surface nutrient replenishment, and to provide new insights on the regulation of the winter–spring phytoplankton blooms by environmental factors.

2. Materials and methods

2.1. Regional setting and study area

The Bay of Calvi (Fig. 1) is located on the western coast of Corsica island, and it opens to the north to the Ligurian Sea, which is one of the main sub-basins of the Northwestern Mediterranean Sea. The bay is influenced by the Modified Atlantic Water of the Western Corsica Current (WCC), flowing northeastwards off the bay, in quasi-geostrophic balance, and following the isobaths (Skliris et al., 2011). The WCC is 20–30 km wide, relatively deep (≈200 m) and stable, even if it is sometimes disturbed by mesoscale phenomena (Bethoux and Prieur, 1983; Millot, 1991; Goffart et al., 1995). It separates the lighter waters on the continental, eastern side from the denser waters of the central Ligurian Sea (Sournia et al., 1990). North of Corsica, the WCC and the more variable Eastern Corsican Current (or Tyrrhenian Current) join together to form the Northern Current, which displays pronounced variations in its seasonal structure and is usually referred to as the Liguro-Provençal current in the Ligurian Sea (Astraldi et al., 1994; Millot, 1999). As far as the pelagic ecosystem is concerned, one of the peculiarities of the Ligurian Sea is that the shelf region is more oligotrophic than the offshore areas (e.g. Sournia et al., 1990; Goffart et al., 1995; Pinca and Dallot, 1995).

The Bay of Calvi is strongly exposed to the dominant southwesterly winds (called Libeccio), and to the less frequent northeasterly winds (called Gregale). The bay is characterised by a narrow continental shelf (mean width ≈ 3 km) and the presence of a deep canyon (mean depth ≈ 600 m) with steep sides (bottom slope up to 40%) that intersects the shelf in front of the city of Calvi. The depth within the bay itself reaches 70 m, and increases rapidly offshore. The presence of the deep canyon at the mouth of the bay enhances shelf-slope exchanges, and influences the circulation within the bay. At the local scale, the mean horizontal current is deviated upstream of the canyon to form an anticyclonic gyre in the western part of the bay and a cyclonic gyre in the eastern part. Average values of current velocity obtained from long-term measurements of the subsurface currents during low wind conditions (wind speed $<4\ m\ s^{-1}$) are of the order of 7 and $5\ 10^{-2}\ m\ s^{-1}$ in the western and eastern parts of the bay, respectively (Djenidi, 1985; Djenidi et al., 1987; Skliris et al., 2001b). In some cases, transient upwelling structures and input of offshore water occur during strong wind events (Brohée et al., 1989; Goffart, 1992; Skliris et al., 2001a).

The Bay of Calvi is a well-preserved, low-runoff system, i.e. local runoff from the Figarella River in the eastern part of the bay is small and irregular, which reflects the stormy Mediterranean precipitation regime. Water quality in the bay is high (Boissery et al., 2013), which is explained by the low anthropogenic pressure, i.e. absence of agricultural or industrial activities, small permanent population (*ca.* 5400 residents), and tourism, which is the main economic activity, limited to July and August. According to years, surface salinity ranges from 37.6 to 38.1 during winter mixing conditions, and nitrate and silicate reach maximum concentrations of 2.0–3.0 μM (same maximum values for the two nutrients) over the whole water column (Goffart, 1992; Goffart et al., 2002). During the stratified period, nutrients are depleted from surface to depth, and the nutrient inputs from runoff or human activities are too low to relax the oligotrophic conditions of the bay. A dense and continuous *Posidonia oceanica* meadow extends on the sandy seabed from 5 to 40 m (Gobert et al., 2003), and photophilic algae colonise the rocky shore from a few centimetres below the surface to 25 m depth (Hoffmann et al., 1992).