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Phytoplankton response to a weak El Niño event

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ABSTRACT

The western coast of South America is a very productive upwelling zone. However, during El Niño events, phytoplankton productivity in the equatorial Pacific declines sharply. A weak El Niño event occurred in 2014. Oceanographic anomalies included an increase in sea surface temperature and water transparency and a decrease in salinity. Phytoplankton composition also changed throughout time reflecting different El Niño stages. Before the El Niño, the community was mainly dominated by species typical of nutrient rich waters, such as large diatoms or silicoflagellates. At the onset of the event, the number of species and the turnover component of beta diversity increased, indicating that previously predominant species now co-occurred with new species transported by warmer surface water masses. At this initial stage, warm water dinoflagellates were indicator species, while a diatom bloom of *Dactyliosolen fragilissimus* indicated nutrient availability and some degree of turbulence in the water column. Finally, the overall abundance of phytoplankton was similar to the homologous months in previous years, but under El Niño conditions the community was dominated by smaller cells. Consequently, primary production attained a minimum, as inferred from the highest values of water transparency. There was no evidence of seasonality. It is concluded that the effect of El Niño on the phytoplankton community in the eastern equatorial Pacific is appreciable even during weak events.

1. Introduction

1.1. General overview

Marine phytoplankton is responsible for almost half of the global primary production on Earth (Field et al., 1998). Ocean primary production varies in response to environmental stressor and other environmental factors like seasonality. Seasonal variations in temperature, depth of the mixed layer, the position of the thermocline or available solar radiation and nutrients are key factors that influence primary productivity in oceans (Venrick et al., 2008; Henson et al., 2013).

The seasonal production cycle in temperate areas is as follows: intense winter mixing replenishes photic zone nutrients, in spring rising temperatures and increased light availability facilitates phytoplankton blooms, while summer induces stratification isolating the well-lit nutrient poor surface waters from sub-thermocline colder nutrient rich waters and finally, fall brings instability to the water column transitioning into a new cycle with winter storms (Chiswell, 2011). Seasonality is not restricted to temperate regions, but rather seasonal patterns have different manifestations in high and low latitude (Chiswell, 2011; Henson et al., 2013). Seasonal patterns also display a meridional component. In the eastern equatorial Pacific, seasonality alternates between two main seasons. The dry season is mainly dominant in August-September and the rainy season has a peak in February-March (Koutavas and Lynch-Stieglitz, 2004). During the dry season cross-equatorial southeast trade winds result in upwelled cold water (Chelton et al., 2001), while decreasing trade winds during the rainy season reduce the intensity of upwelling, promoting increased sea surface temperatures (SST) (Koutavas and Lynch-Stieglitz, 2004). This cycle is closely associated with the seasonal north-south migration of the Intertropical Convergence Zone (ITCZ), which attains its northernmost position during the dry season and moves south during the rainy season, though it is rarely centered below the Equator (Waliser and Gautier, 1993).

Seasonal variation in the eastern tropical Pacific reflects sub-decadal El Niño/Southern Oscillation (ENSO) variability. ENSO is a manifestation of atmospheric pressure gradients and heat flux dynamics between the ocean and the atmosphere in the Pacific Ocean (Kao and Yu, 2009; Stramma et al., 2016). It comprises cycles of warm and cold events of varying intensity, sometimes with worldwide environmental and economic effects (McPhaden et al., 2006). A warm ENSO phase is simply known as El Niño and is evidenced by warmer SST and low sea level pressure anomalies in the equatorial eastern Pacific (Wang and

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Fiedler, 2006). Together with the climatic regime described for the rainy season (Koutavas and Lynch-Stieglitz, 2004), trade winds during El Niño weaken along the equator, as atmospheric pressure rises in the western Pacific. Conversely, atmospheric pressure falls in the eastern Pacific, where the thermocline becomes deeper with the arrival of warm superficial waters from the west (McPhaden et al., 2006). The ENSO's cold phase, known as La Niña, results in the elevation of the thermocline in the eastern equatorial Pacific, while upwelled nutrient-rich deep waters lower SST (Ryan et al., 2006).

El Niño events affect population dynamics and/or the distribution of a variety of marine organisms, such as zooplankton species, scallops, shrimps, fishes, pinnipeds, and sea birds, including penguins and cetaceans in the eastern Pacific (McPhaden et al., 2006; Wang and Fiedler, 2006 and references therein). The reduction in upwelling intensity and the enhancement of stratification during El Niño events reduces primary production, affecting the transfer of energy to higher trophic levels (McPhaden et al., 2006; Bakun et al., 2015).

Margalef (1978) considered nutrient supply and turbulence as the most important factors changing phytoplankton species, through natural selection and evolution. Furthermore, this author stated that nutrient input is usually associated with turbulence, thereby favoring a single set of strategies (such as motility, heterotrophy or defensive mechanisms against grazers), because species adapted to a high concentration of nutrients are also adapted to higher turbulence. Although some authors assign a direct effect of temperature upon productivity and composition of marine phytoplankton communities (Thomas et al., 2012), Marañon (2015) claims that changes in resource supply rather than temperature determine biogeographic patterns in phytoplankton size structure and growth rate. This author adds that phytoplankton metabolic temperature sensitivity, under nutrient limitation, decreases or even disappears entirely. Therefore and in accordance with Margalef (1978), species adapted to nutrient deficient environments may also be demonstratively adapted to stratification, which may even require some form of motility. As such, temperature would be a proxy, rather than the main driver explaining both cell size reduction and compositional changes during El Niño events (Rousseaux and Gregg, 2012).

Compositional shifts in phytoplankton communities are expected with ENSO oscillations. Sometimes they are observed and quantified, though in certain cases results do not match expectations (Strutton et al., 2008; Venrick et al., 2008). Changes and shifts in species composition are linked to beta diversity (Baselga, 2010). Variability in beta diversity may be explained by factors such as environmental gradients, biological interactions (predation, for instance) or species dispersal (Reynolds, 2006). Changes in phytoplankton species composition are deeply tied to substantial oceanographic changes (Margalef, 1978; Strutton et al., 2008; Marañon, 2015). Yet, small-scale oceanographic differences may also play a major role in structuring patterns of phytoplankton beta diversity (Mousing et al., 2016). As such, both phytoplankton diversity and drivers controlling species occurrence in time and space are important research topics in marine ecology.

1.2. El Niño anomalies in the study area

The study area is located in the Niño 1 + 2 region. This was the first oceanic region where El Niño was studied, afterwards extended to regions Niño 3, Niño 4 and Niño 3.4 in the Pacific Ocean (Kao and Yu, 2009). Time series of SST and their anomalies for all these oceanic regions (Fig. 1) are freely available at the Climate Prediction Center website (http://www.cpc.ncep.noaa.gov/data/indices/sstoi.indices). Anomalies are calculated as deviations from the 1981–2010 monthly SST values, and may be positive or negative. Anomaly profiles between 2014 and 2015 (El Niño years) are more similar than between 2014 and 2013 (the latter was not an El Niño year, Fig. 1; Stramma et al., 2016; Yukiko et al., 2016). Profiles suggest similar oceanic processes between 2014 and 2015, albeit with different intensities. In fact, a strong El Niño was expected in 2014, but an intrusion of subsurface cold water off the

tropical Pacific is thought to have weakened its manifestation (Yukiko et al., 2016). The observed anomalies increased in consecutive sampling occasions (arrows in Fig. 1) suggesting a heating process through time. Differences in the values of the anomaly for the same month in consecutive years (first and last arrow in Fig. 1) suggest different oceanographic conditions in the study site. This tendency evolved throughout time, with the highest anomaly values recorded in October 2015, when a strong El Niño event occurred (Stramma et al., 2016). SST profiles are also similar between 2014 and 2015, with higher values in 2015, while 2013 SST had a different annual pattern when compared with the following years (Fig. 1).

The purpose of this study is to investigate changes in both the environmental conditions and the phytoplankton assemblages associated with a weak El Niño event occurred during sampling. Environmental variables such as changes in temperature, salinity or Secchi disk depth over time were considered to determine whether phytoplankton assemblage dynamics were constrained by the measured environmental variables, that is, if consistent changes in the phytoplankton community were a real time response to the environmental conditions induced by a weak El Niño. It is also hypothesized that environmental changes associated with the arrival of El Niño should affect beta diversity as compositional changes (turnover) would reflect adaptation of the community to new environmental conditions. Finally, species significantly related to different El Niño stages were identified in an attempt to highlight indicator species.

2. Material and methods

2.1. Study area

The Ecuadorian coast is a complex area where four marine currents converge in the equatorial eastern Pacific (Fig. 2). The warm current of Panama, coming from the north, is characterized by high temperature, low salinity and low nutrient concentrations; it is strongest in the rainy season (from January to April). The Peruvian Coastal Current (Humboldt) flows northwards and is characterized by cold nutrient-rich water with high levels of salinity and chlorophyll (Fiedler and Talley, 2006; Lavin et al., 2006; Pennington et al., 2006). The latter current promotes fisheries and is especially intense during the dry season, from July to November, partly reflecting the seasonal cycle of the austral winter. Additionally, the convergence of the Northern Equatorial Countercurrent (NECC) and the South Equatorial Current (SEC) forms a transition zone called Equatorial Front (EF) whose latitudinal position varies throughout the year. The westerly NECC is characterized by warm waters of low salinity. In turn, the SEC flows northwest and crosses the equator to latitude 5°N where it turns westwards. The EF is sometimes vigorous off the Ecuadorian cost. It has lower temperature, salinity and nutrient concentrations than the NECC, but higher concentrations of chlorophyll (Fiedler and Talley, 2006; Pennington et al., 2006).

2.2. Sampling and laboratory procedures

The sampling sites corresponded to seven fixed sampling stations located 18.52 km off the Ecuadorian shore. From north to south, they are named Esmeraldas, Pedernales, Crucita, Pto Lopez, Salinas, Anconcito and Pto Hualtaco (Fig. 2). The average linear distance between stations was 83.67 ± 29.97 km (mean \pm sd). The maximum depth varied among sampling sites due to the geomorphology of the continental shelf. A maximum depth ranging from 100 m to 150 m was recorded in front of Esmeraldas, Puerto Lopez, Salinas and Anconcito, while lower depths were registered at Crucita and Pedernales (80 m and 53 m, respectively). Pto Hualtaco had the lowest depth (25 m). GPS was used to determine the position of the sampling sites.

Sampling was carried out during the dry season (October 2013 and 2014) and the rainy season (April 2014) using an outboard motorboat

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