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Ocean-lagoon water and plankton exchanges in a semi-closed pearl farming atoll lagoon (Ahe, Tuamotu archipelago, French Polynesia)

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ABSTRACT

In atoll lagoons, plankton richness is highly dependent on water exchange with the ocean through the atoll rim. However, the dynamics of the physical and biological fluxes at the lagoon-ocean interface remain poorly characterized. Here, we studied the combined effects of lagoon-ocean water exchanges and local environmental conditions on the phyto- and zooplankton abundance and community structure across the atoll lagoon rim of Ahe (Tuamotu Archipelago, French Polynesia). Plankton and environmental variables were monitored in May 2013 (i) at several stations inside and outside the lagoon and (ii) during time-series corresponding to ebb-flood tidal cycles in the two types of channels connecting the lagoon to the ocean: at the passage (300 m long and about 11 m deep) and in *hoa* (i.e reef-flat less than 50 cm depth). Our results highlight tidally-driven selective plankton exchanges between the lagoon and external ocean. Phytoplankton (chlorophyll-a) and zooplankton biomass were respectively 4 times and 7 times higher in the lagoon than at stations outside the atoll lagoon. Copepoda was the dominant zooplankton group at the oceanic station (>75% abundance) whereas meroplankton (with bivalve larvae most common) was dominant at the lagoon stations (54%), in the passage (55–82%) and in *hoa* (>80%). These differences between sites suggest a loss of bivalve larvae through export to the ocean and retention and/or increased production of copepods in the lagoon. The daily export of bivalve larvae represents a low percentage of the lagoon stock, in agreement with previously published larval dispersal numerical models. The retention of copepods could constitute a significant input of nutrients and organic matter (through excretion, feces release, decomposition, and remineralization) into the lagoon.

1. Introduction

Coral reef lagoons are some of the marine ecosystems with the greatest biodiversity. They provide many goods and services to human populations on a local, regional and national level (shelter from high energy weather events, fisheries, aquaculture, tourism, biochemicals and drugs of natural origin, etc.). Lagoons and their resources are also frequently impacted by uncontrolled development combined with climate change (Bell et al., 2011). Atolls are one of the major type of coral reef systems, generally characterized by a prominent central lagoon (Goldberg, 2016). Atoll lagoons are relatively high productive, compared to the oligotrophic surrounding ocean (Hatcher, 1997), which explains why they have been frequently used for aquaculture purposes. In the Tuamotu Archipelago, the culture of *Pinctada margaritifera* pearl oyster is the main source of income for French Polynesia after tourism. This industry relies on spat collection, and on the farming and grafting of adult oysters that are left suspended in lagoon waters till the pearls can be collected. Pearl farming is totally dependent on phytoplankton standing biomass and production which is the main food source for larval, juvenile and adult oysters (Doroudi et al., 2003; Loret et al., 2000; Andréfouët et al., 2012a). Zooplankton is also important for pearl-oyster production as pearl-oyster larvae (i) are a major component of the meroplankton, (ii) have to compete for food with other filter-feeding zooplankton (e.g. small copepods), and (iii) are prey for zooplanktonic predators (e.g.

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chaetognaths) (Pagano et al., 2012). The initial success and sustainability of the pearl farming industry is thus dependent on the lagoon trophic network and planktonic richness and biomass.

Atoll lagoon planktonic richness cannot be related to terrigenous inputs as in the case of coral reef lagoons bordering islands or continents (Carassou et al., 2010). Several studies showed that phytoplankton biomass is related to lagoon water residence time (Delesalle and Sournia, 1992; Andréfouët et al., 2001). Reef and lagoon productivity can be explained by high nutrient recycling through coral symbiotic organisms and microbial food webs (Hinde, 1988; Atkinson et al., 2001; Falter et al., 2004). Primary production may be also partly supported by nitrogen-fixing organisms (Charpy-Roubaud, 2001) and by efficient recycling of nutrients, especially in pearl oyster farming lagoons (Lacoste et al., 2014; Lacoste and Gaertner-Mazouni, 2016). According to Charpy (2001), phosphate flux from the ocean may fulfill the requirements of reef and lagoonal communities. Zooplankton retention/aggregation in the lagoon linked to their behavioral responses to tidal-currents (swimming against the flow, downwards migration to the low current region and/or active substrate attachment) may also lead to carbon enrichment (Alldredge and Hamner, 1980; Genin et al., 2005; Shang et al., 2008; Leichter et al., 2013).

Ahe atoll is one of the main French Polynesia atolls for research on pearl oyster aquaculture and lagoon environments (Andréfouët et al., 2012a). In a study performed at three different seasonal periods in 2008–2009, we showed that in this atoll lagoon the dynamics and spatial distribution of metazooplankton communities and pearl oyster larvae were mainly driven by wind-induced circulation and, to a certain extent, by tides (Thomas et al., 2012; Pagano et al., 2012). However, the dynamics of the plankton flux at the lagoon-ocean interface and according to the ebb/flood cycle was not investigated. Here, we aim to fill this gap, and we studied more specifically the combined effects on plankton of lagoon-ocean tidal exchanges and local environmental conditions. This study focuses on zooplankton, with explicit consideration of its taxonomic components, while phytoplankton is only characterized by its chlorophyll and photosynthetic pigment composition. A complete description of the phytoplanktonic communities will be presented elsewhere.

2. Methods

2.1. Study site and sampling strategy

The Ahe atoll (14°29′ S; 146°18′ S) is located in the northwestern part of the Tuamotu Archipelago in the Pacific Ocean. The atoll dimensions are 23.5 km long and a maximum of 12.2 km wide (Fig. 1). The 142 km^2lagoon has a maximum depth of 70 m in the central zone. The atoll rim surrounding the lagoon is not completely closed: there is a narrow passage, the Tiareroa Pass (300 m long and about 11 m deep) to the northwest, and several reef-flat spillways (channels less than 50 cm deep, called "*hoa*" in polynesian) mostly on the southern and northwestern side of the rim. The climate is wet tropical with one rainy season from November to April. Maximum precipitation occurs in December and January. The annual air temperature variation is low (25–29 °C) with a regular seasonal trend. The wind regime is dominated by moderate easterly trade winds year-round, with strong south wind in the austral winter, and western gales that can occur in the warm season till May (Thomas et al., 2014; 2016). Sea-surface temperature (SST) in the Tuamotu region ranges between 26 and 30 °C with highest values from November to May, but this pattern can be modified by ENSO events (La Niña/El Niño). Our study period (May 2013) corresponds to the end of the hot season in a normal year according to climatic conditions (OSTIA; http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html).

The tide is semi-diurnal with small amplitudes (mean tidal range = 50 cm, 31 cm neap tide and 73 cm spring tide), due to the proximity in the region of a M2 amphidromic point (Dumas et al., 2012).

Sampling was carried out in May 2013 from R/V Alis during the POLYPERL campaign. We considered four sites (Lagoon, Ocean, Hoa, Passage) with different stations that are each sampled with a different frequency (Figs. 1 and 2):

- In the lagoon, three stations (stations L1, L2, and L3; 23 m, 50 m and 45 m deep respectively) were sampled once between 07:00 and 10:00 (i.e., in ebb or slackwater situations) on May 1st, 11th, 17th, 21st and 24th;
- At the passage, the station P (10 m depth) was sampled for a time-series corresponding to flood-ebb sequence with one sample every hour between 07:00 and 13:00 on May 7th;
- Inside *hoa*, stations H1 and H2 (<1 m depth), were located in the south-west and in the south-east of the atoll, respectively. H1 was sampled once during flood conditions on May 9th (the ebb sample was lost) while H2 was sampled twice during ebb and flood conditions on May 14th,
- Three outer oceanic stations were sampled with two stations off H2 (stations OC1 and OC2, sampled on May 5th) and one station located directly off the passage (station OC3, sampled on May 25th). Depth at these stations was>400 m.

The tidal situation (water height) corresponding to the different samplings in the lagoon, ocean, passage and *hoa* are shown in Fig. 2.

The time series at the passage (May 7th) aimed at estimating ocean - lagoon exchanges along a tidal cycle. However we could not sample along a whole cycle (i.e., between two successive identical tidal situations), due to safety reasons: at some point during the flood the stationary waves in the pass generated by in-going current meeting the shallowest area of the pass was too unsafe for sampling, for both people and gear (e.g., a plankton net was lost at the first attempt to sample in these conditions).

2.2. Environmental and trophic variables

Ocean water level values during our study were obtained from the hydrographic and oceanographic office of the French Navy *(Service Hydrographique et Océanographique de la Marine;* http://www.shom.fr/*)*. Wind speed (WS) and direction (WD) were recorded hourly by a meteorological station located on the R/V Alis.

In the ocean and in the lagoon, salinity and temperature were recorded using a CTD SBE 19+, from surface to bottom. Water samples were collected at two depths in the lagoon (10 and 20 m at L1, 10 and 40 m at L2 and L3) and also at two depths (5 m, 40 m) for the oceanic stations, using a 5 L Niskin bottle. At the passage and in the *hoa*, water samples were collected just below the surface (0.5–1 m).

Nutrients (nitrate + nitrite reported as NOx, and phosphate) were analyzed post-expedition on $HgCl_2$ preserved samples (Kattner, 1999) at the IRD Nouméa center (New Caledonia). Determinations were performed by colorimetry using an Autoanalyzer AA3 Bran + Luebbe (Strickland and Parsons, 1972).

Chlorophyll *a* (Chl *a*) concentrations of particles retained on Whatman GF/F filters were measured immediately on board R/V Alis on 250 ml water samples using a Turner Designs TD 700 fluorometer after methanol extraction (Welschmeyer, 1994). Size-fractionated Chl *a* were also measured on 400 mL samples using 2 μm Nuclepore membranes. The fraction of Chl *a* not retained by a 2-μm membrane (Chl *a* < 2 μm) was assigned to the picophytoplankton biomass. This picoplanktonic fraction was not measured