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Metazooplankton communities in the Ahe atoll lagoon (Tuamotu Archipelago, French Polynesia): Spatiotemporal variations and trophic relationships

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Abstract:

Metazooplankton abundance, biomass (<80 μm, 200–500 μm and >500 μm) and community structure in the Ahe atoll were studied together with their relationships with environmental factors (temperature, salinity, wind) and trophic factors (phytoplankton, bacteria, heterotrophic nanoflagellates (HNF) and ciliates) during three periods in 2008–2009. Meroplankton, mainly bivalve and gastropod larvae, was dominant. Holoplankton was dominated by copepods, the main species being *Oithona* spp., *Paracalanus parvus*, *Clausocalanus* spp., *Corycaeus* spp., *Acartia fossae* and *Undinula vulgaris*. The results suggest a clear wind influence on the structure and horizontal distribution of the zooplankton communities. The metazooplankton appeared to be controlled mainly by food resources, suggesting a bottom-up control. The low nanophytoplankton biomass in contrast to the high abundance of picophytoplankton, HNF and nano-particle grazers (mainly *Oithona* spp., *Paracalanus* and bivalve larvae) highlighted the importance of the microbial loop in the food web.

Keywords : Metazooplankton ; Spatio-temporal patterns ; Trophic relationships ; Pearl oyster ; Atoll lagoon ; French Polynesia

1. Introduction

Metazooplankton plays a major role in the functioning and productivity of aquatic ecosystems through its impact on nutrient dynamics and its key position in food webs. Most mesozooplanktonic organisms exert a strong grazing impact on the phytoplankon and on the microzooplankton (Pont, 1995; Calbet, 2008). They are also a food source for organisms of the upper trophic levels such as planktivorous fish and carnivorous invertebrates (Pinel-Alloul, 1995). In coral reef and atoll lagoon environments, they are important contributors to the benthic and pelagic food webs (Bozec et al., 2004; Alldredge and King, 2009). Zooplankton organisms can also be used as biological indicators for pollution, water quality and eutrophication (Attayade and Bozzelli, 1998; Webber et al., 2005). Their generation times may be short enough to respond quickly to acute stress but long enough to integrate the effects of chronic problems. These attributes can be useful to design a community ecosystem health indicator (Cairns et al., 1993). However, very few studies have dealt with zooplankton in atoll lagoons (Gerber, 1981) and only a few have concerned the Tuamotu Archipelago (Michel et al., 1971; Ricard et al., 1979; Le Borgne et al., 1989; Carleton and Doherty, 1998).

Coral reef and atoll lagoons are productive ecosystems, compared to surrounding ocean (Hatcher, 1997). They have been frequently exploited for aquaculture, as in the Tuamotu Archipelago (French Polynesia) where pearl oyster farming is a major driver of the local economy (Andrefouët et al. this issue). The planktonic pearl-oyster larvae mainly feed on nanophytoplankton with high ingestion rates (Douroudi et al., 2003). The adults, cultivated in sub-surface pelagic nets, are also important passive consumers of nanoparticles (Yukuhira et al., 1998; Fournier et al. this issue). Farmed pearl-oyster populations can be considered as components of the pelagic ecosystem in pearl farming lagoons. In these ecosystems, they share (and may compete for) food resources with several pelagic components (including zooplankton) and may serve as food for other ones. Studying the different communities of the pelagic ecosystem and evaluating their stocks and their inter-relationships are required to define the optimal conditions for the recruitment and development of oysters. This information is also necessary to determine the load capacity for cultivation (Niquil et al., 1998).

A multidisciplinary research program was funded by the European Development Fund (EDF) in 2007 to describe, among other goals, the ecological environment of the pearl-oyster *Pinctada margaritifera* (Linnaeus, 1758) and its relationship with the pelagic trophic network.

Our study is part of this multidisciplinary study on the trophic environment of *Pinctada margaritifera*. It aimed at analyzing within a farmed lagoon the spatiotemporal variations of metazooplankton standing stock and community composition according to the main environmental and trophic parameters.

2. Methods

2.1. Study site and sampling strategy

The Ahe atoll (14°29' S; 146°18' S) to the north west of the Tuamotu Archipelago in the Pacific Ocean is 23.5 km long and a maximum of 12.2 km wide (Fig.1). The lagoon is 142 km^2 in area with maximum depth of 70 m in the central zone. The atoll rim which surrounds the lagoon is not completely closed: there is a passage (300 m long and about 20 m deep) to the northwest between the lagoon and the ocean, and several spillways mostly in the southern part of the rim. The climate is wet tropical with one rainy season from November

to April with the maximum precipitation being in January and December. The annual air temperature variation is low (25-29°C) with a regular seasonal trend. The dominant winds (NE trade-winds) are strongest in October-November.

Meteorological data (monthly averages of air temperature, rainfalls, and wind speed) were available from the meteorological station of Takaroa (Tuamotu; 14°28' S - 146°2' W) for a period bracketing our surveys, in 2007-2009 (Fig. 2). The station is only 130 km from Ahe (see Fig 1) and given the lack of any orographic effects on these low lying islands, Takaroa data were deemed representative of the conditions in Ahe atoll.

Three sampling surveys were carried out in May 2008, October 2008 and February 2009. During each period, four lagoon stations (St 1, 23 m depth, St 3, 50 m depth, St 9, 50 m depth and St 11, 45 m depth) were sampled on 2 (October 16 and 20, 2008) and 3 (May 14, 20 and 23, 2008; February 17, 20 and 24, 2009) occasions.

2.2. Environmental and trophic variables

Vertical profiles of salinity and temperature were recorded using a YSI 600 probe, from surface to bottom. Water samples were collected at two (0.5, 10 m; stations 1 and 11) and three (0.5, 10 and 20 m; stations 3 and 9) depths using a 5 L Niskin bottle. Chlorophyll *a* (Chl a) concentrations of particles retained on Whatman GF/F filters (0.7 µm of porosity) were measured on 400 ml water samples using a Turner Designs TD 700 fluorometer after methanol extraction (Welschmeyer, 1994). Particle fractionation using 2 µm pore size Nuclepore membranes gave an estimate of Chl a concentration for 0.7-2, and >2 µm size classes. The fraction of Chl a not retained by a 2-µm membrane was assigned to picophytoplankton biomass.

Bacteria and picoautotrophic cells were fixed with 0.2 µm filtered formaldehyde (final concentration 2%) and frozen in liquid nitrogen. Bacterial cells were enumerated by flow cytometry using the method described by Marie et al. (1999). A 1 ml formaldehyde-fixed subsample was incubated with DAPI at a final concentration of 1/10,000 for 15 min at room temperature in the dark. Each subsample was counted using a MoFlo cytometer (DAKO). Stained bacterial cells, excited at 488 nm, were enumerated according to their right-angle light scatter (RALS) and green fluorescence (FL1) measured using a 530/30 nm filter. These cell parameters were plotted onto 1024 channels and recorded on a 4-decade logarithmic scale. Fluorescent beads (0.94 µm, Polysciences Inc., Warrington, PA, USA) were added to each sample. Standardized RALS and FL1 values (RALS and FL1 for the cells divided by the RALS and FL1 for 0.94 µm beads,) were used to estimate the relative size and nucleic acid content of the bacterial cells (Troussellier et al*.,* 1999). The list mode files were analyzed using SUMMIT software (Dako Colorado Incorporation).

Picophytoplankton (*Prochlorococcus sp.* and *Synechococcus sp.* cells) and autotrophic picoeukaryotes counts were performed using the same flow cytometer. Cells excited at 488 nm were detected and directly enumerated according to their FALS and RALS properties and their orange (585/42 nm) and red fluorescence (>650 nm) from phycoerythrin and chlorophyll pigments, respectively. Fluorescent beads (0.94 µm) were also added to each sample. The list mode files were analyzed using SUMMIT software (Dako Colorado Incorporation).

For microzooplankton enumeration (ciliates), water samples (1 liter) were fixed with alkaline lugol iodine (2% final concentration). A first sedimentation was conducted for 24h and the top 900 ml of the samples was slowly siphoned off using small-bore tubing. The remaining 100 ml was then stored at 4°C in the dark before enumeration. After sedimentation in a Utermöhl settling chamber (Hydro-Bios combined plate chamber), cells were enumerated at a magnification of x200 using a Zeiss axiovert inverted microscope with interference contrast.

Nanoflagellates (in 25 ml water samples) were fixed with buffered paraformaldehyde (final concentration 1%), stained with DAPI (2.5 x 10^{-4} g.l^{-1} final concentration) and counted on 0.8 µm black polycarbonate filters by epifluorescence microscopy (Sherr et al.; 1994). Heterotrophic nanoflagellates (HNF) were distinguished from pigmented (autotrophic) nanoflagellates (PNF) by the absence of chlorophyll fluorescence.

The following factors were used to convert abundance into carbon biomass:

Bacteria: 14 fgC/cell (Gundersen et al., 2002).
Prochlorococcus: 60 fgC/cell (Charpy and Blanchot, 1998).
Synechococcus: 178 fgC/cell (Charpy and Blanchot, 1998).
Picoeukaryote: 836 fgC/cell (Verity et al., 1992).
Nanoflagellates: 3140 fg C/cell (Pelegri et al., 1999).
Ciliates: 2318 pgC/cell (Putt and Stoecker, 1989).

2.3. Zooplankton

Zooplankton was sampled by vertical hauls (bottom to surface) using a 80 µm mesh-size WP2 net equipped with a Hydrodata flowmeter. Each sample was divided into two equal sub-samples using a Motoda-type splitter. One sub-sample was used for biomass measurements and the second was fixed with formaldehyde at 4% final concentration and used for identification and enumeration of the taxa. Biomass measurements (dry weight, DW, 60°C desiccation during 48 h; Lovegrove, 1966) were made after size-fractionation using 80 µm, 200 µm, 500 µm and 1000 µm nylon sieves. The taxa were identified and enumerated using sub samples taken by wide bore piston pipettes (0.5 to 5 ml). At least 100 individuals of the main taxa were counted in each sub-sample under a dissecting microscope (Olympus SZX200, magnification x200 to x500). The rarest taxa were estimated from the whole sample. Zooplankton taxa were identified according to Tregouboff and Rose (1957), Razouls et al. (2005-2011) and Conway et al. (2003).

The individual weight of each taxon was estimated from their size measured under a dissecting microscope (objective 50, ocular 10). The organism carbon weights were then estimated using the length-weight relationships found in the literature (Uye, 1982; Chisholm and Roff, 1990; Mauchline, 1998; Douroudi et al., 2003). The size were considered as: prosome length for copepods, from the eye base to the junction of abdomen and telson for euphausiids, from the base of the head to the base of junction of abdomen and telson for amphipods, the anterior nectophore length measurement for siphonopores, shell length for bivalve larvae and total length for other taxa.

2.4. Data analysis

Correlations between zooplankton abundance and environmental factors were computed using Statistica V6 software. The significance of each correlation was examined after Bonferroni correction for the effects of multiple comparisons.

The spatial and temporal variability of environmental variables and zooplankton communities was assessed by multivariate analysis. Two data sets were considered: the abundance of all the zooplankton taxa identified and the environmental variables. Factorial correspondence analysis (FCA) was performed on the first data set and principal component analysis (PCA) on the second. The results of the two analyses were associated by co-inertia analysis (Dolédec and Chessel, 1994). A cluster classification of observation scores from the first factorial plane was applied to partition taxa and stations (Ward's aggregation criterion). Analyses were performed using ADE4 software (Thioulouse et al., 1997).

The spatial and temporal variability of the trophic groups (biomass as µg C L^{-1}) was assessed by PCA. The groups considered were picophytoplankton (*Prochlorococcus sp.*, *Synechococcus sp,* and picoeukaryotes), autotrophic nanoflagellates, bacteria, heterotrophic nanoflagellates (HNF), ciliates, predators (chaetognaths, medusae, ctenophores, *Labidocera* spp, *Candacia* spp, *Corycaeus* spp, *Oncaea* spp and fish larvae), picoparticle feeders (salps and appendicularians), bivalve larvae and other nanoparticle feeders (other metazooplankton organisms). Picoparticle feeders, nanoparticle feeders and predators were distinguished according to Ohtsuka and Onbe (1991), Turner (1984) and Mauchline (1998).

All analyses were performed on log X+1 transformed data.

3. Results

3.1. Environmental and trophic variables

Different meteorological conditions were observed during the 3 sampling periods (Fig. 2). Rainfall were high in February 2009 (70 mm $month^{-1}$) compared to May and October 2008 (52 and 23 mm $month^{-1}$, respectively). Wind speed was lower during the May 2008 survey (0 to 7.7 m s^{-1} during the sampling period) than for the other surveys (6.1 - 11.5 m s^{-1} and 3.0 - 11.5 m s^{-1} in October 2008 and February 2009 respectively). Water temperature and salinity showed significant variations between sampling seasons (Fig. 3). The lowest salinity and highest temperature were recorded in February 2009, during the rainy season. In May 2008, at the beginning of the dry season, mean salinity and temperature were high while temperature was minimal in October 2008, at the end of the dry season.

Total Chl *a* was higher in May and February than in October and relative contributions of the two fractions (Chl *a* < 2µm and >2µm) were similar between periods (Fig. 4a). The smaller fraction (Chl *a* < 2µm) was always dominant, representing 72 to 82% of the total. In May and October (dry season), stations 1 and 11 displayed higher Chl *a* concentrations than stations 9 and 3. The total autotrophic organism biomass (picoeukaryotes, *Synechococcus* and pigmented nanoflagellates, PNF) had the same spatial patterns as chlorophyll in May and February but not in October (Fig 4b). The PNF fraction was very high in May, whereas the *Synechococcus* fraction was very high in October and February. The heterotrophic microorganism biomass was more balanced between groups (bacteria, HNF and ciliates) in May than in October and February (predominance of HNF) (Fig 4c).

3.2. Zooplankton

42 taxa were identified in the samples, 31 holoplanktonic (18 Copepods, including copepod nauplii, and 13 other organisms) and 11 meroplanktonic ones (Table 1). Copepods were the most abundant group among the holoplankton, the main taxa being *Oithona spp.*, Paracalanidae (*Paracalanus parvus* and *Clausocalanus spp.*), *Corycaeus spp.* and *Acartia fossae*. The other holopankton taxa were mainly appendicularians, chaetognaths and pteropods (*Limacina spp.* and *Creseis spp.*). Meroplankton comprised mainly bivalves (including *Pinctada margaritifera*) and gastropod larvae.

Meroplankton was more abundant than holoplankton in almost all the stations (mainly due to the number of bivalve larvae) except at stations 1 and 3 in October 2008. Zooplankton total abundance (Table 1) and biomass (Fig. 5) were strongly correlated ($r=0.74$; $p=0.0058$). They were both higher in February 2009 than in May and October 2008 (Fig 5 a and b). They also displayed the same spatial pattern in May 2008 with higher values at stations 1 and 11 than at stations 3 and 9, for all biomass size-fractions and taxa (Fig 5 a and b).

3.3. Relationships between zooplankton and environmental variables

3.3.1. Correlation analysis

Total zooplankton abundance was positively correlated with temperature, total and <2µm Chl *a* and ciliates (Table 2). Total meroplankton and bivalve larvae abundances were positively correlated with total and <2µm Chl *a*. Copepod, bivalve larvae and meroplankton abundances as well as total biomass and all size-classes showed no significant relationship with any of the environmental and trophic variables. Other holoplanktonic organisms showed significant negative correlations with salinity and bacteria.

There were positive correlations between biomasses of the various functional metazooplankton groups (predators, nano and picoparticle feeders) except for bivalve larvae (Table 3). Predators were significantly and negatively correlated to the biomasses of bacteria and PNF and positively to picophytoplankton and HNF.

3.3.2. Multivariate analysis

The first factorial plane of the co-inertia analysis explained 88% of the variance, mainly on the first axis (60%). In both systems (Environment and Zooplankton), the first axis showed a seasonal distinction between the May 2008 survey (M1, M3, M9 and M11) and the two other surveys (October 2008 and February 2009) (Fig 6). May samples were characterized by high salinity and high PNF and bacteria abundance. They were also associated with several copepod taxa: Candacia spp., *Labidocera* sp. and *Oithona plumifera* and with salps, ctenophores, isopods, foraminifers and water mites. Values recorded in October and February were correlated with HNF, *Synechococcus*, *Prochorococcus* and picoeukaryotes and with several zooplankton taxa including harpacticoid (*Microsetella* sp, *Tisbe* sp and undetermined genera) and cyclopoid (*Oncaea* sp.) copepods, medusae, annelid and cirriped larvae. The second axis mainly opposed the February survey (on the top of the axis) to the October survey (on the bottom) and, within each survey, station 1 (top) to the other stations. The February survey and station 1 were characterized by higher temperature, chlorophyll, picoeukaryote and ciliate values and by several rare zooplankton taxa such as ctenophores, *Lucifer* spp., isopods, water mites, Cirriped and Actinotroch larvae.

In the PCA of the trophic-functional groups, the first factorial plane explained 89% of the variance, mainly on the first axis (67%). The first axis showed a clear opposition between the May 2008 survey which was characterized by high PNF and bacteria abundances and the surveys in February 2009 (mainly) and October 2008 (to a lesser extent) which were characterized by high picophytoplankton and HNF abundances and by the functional zooplankton groups (predators, pico- particle feeders, bivalves and other nano-particle feeders) (Fig. 7). It is also interesting to note the associations between HNF and picophytoplankton, between particle feeders and predators and between bivalve larvae and ciliates.

4. Discussion

4.1. Hydrobiological context

The phytoplanktonic biomass, as inferred from Chl *a*, measured in the Ahe lagoon was comparable to that in other oligotrophic ecosystems and similar to that in other lagoons of the Tuamotu Archipelago (Rancher and Rougerie, 1995). The proportion of picoplankton was close to that recorded in other atoll lagoons and in agreement with additional measurements in Ahe made in 2009 and 2010 (Charpy, 1996, Charpy et al. this issue).

High spatio-temporal variations of chlorophyll, autotrophic (picoeukaryotes, *Synechococcus* and autotrophic nanoflagellates, PNF) and heterotrophic (bacteria, HNF and ciliates)

organisms were observed (see Fig. 4). A large part of this variability may be linked to water circulation within the lagoon and with the exchanges with the ocean, as discussed by Lefebvre et al. (this issue) for photosynthetic parameters. Dumas et al. (this issue), using one year field data and a 3D hydrodynamic model, showed how the wind influences the water circulation in Ahe atoll. They identified 3 residual circulation cells when climatological wind is activated: the south and north cells (including stations 1 and 11 respectively) with a residence time longer than in a central cell (including stations 3 and 9) more directly under the influence of the pass. In October 2008 and February 2009 during high wind speed condition from the east (7-9 m^{-s}), the observed little difference between stations may be the consequence of water homogenization by the overturning lagoon-scale current that may affect in the same way the depth sampled here (0-10, and 0-20m depending on stations). In May, the clear spatial differences of chlorophyll and autotrophic organisms between central (stations 3 and 9) and coastal (stations 1 and 11) stations may be partly explained by lighter winds (< 2-4 m^{-s}) stronger pass influence, and by the difference in residence time between the atoll sectors, as suggested by Lefebvre et al. (this issue). The effect of wind on biological properties was already shown by Charpy and Charpy Roubaud (1991) and by Torréton et al. (2007).

The incidence of pearl farming on the variability of microorganisms can also be pointed out as suggested by Lefebvre et al. (this issue). In May, the highest biomass values were observed at station 1, in the more confined, southwest shallow area of the lagoon where pearl farming is more intensive. The highest chlorophyll values reported there correspond to highest phytoplankton production values provided by both Charpy et al. (this issue) and by Lefebvre et al. (this issue). According to Loret et al. (2000) for Takapoto Atoll, these observations could be linked to the recycling of nutrients by pearl oysters.

4.2. Zooplankton community: dominance of meroplankton and bivalve larvae

The mean total zooplankton biomass and abundance in the Ahe lagoon were similar to those found in other Tuamotu atolls (Ricard et al.; 1979; Le Borgne.et al., 1989). Furthermore, the holoplanktonic community (dominated by the copepods *Oithona* spp., *Paracalanus parvus* and *Clausocalanus* spp., *Corycaeus* spp., *Acartia fossae and Undinula vulgaris*) was very close to those described in other atoll lagoons of the Tuamotu Archipelago in previous studies (Rose, 1953; Michel, 1969; Michel et al., 1971; Le Borgne et al., 1989; Sakka et al., 2002) and in other lagoon ecosystems in the Pacific Ocean (Le Borgne et al., 1997; Carassou et al., 2010). However, the proportion of meroplankton (35% to 74%) and bivalve larvae (19% to 56%) to total zooplankton was higher than observed in Takapoto (1 % and < 0.7% respectively; Sakka et al., 2002) and in Tikeau (12-19 % and 11-14% respectively; Blanchot et al., 1989; see their Tables 4 and 6) or in other coral reef lagoons (eg 15% and 4% respectively in New Caledonian lagoon; Carassou et al., 2010).

In Ahe lagoon, linked to pearl farming, *Pinctada margaritifera* could constitute a large part of this important bivalve larvae stock, but Thomas et al. (this issue, a) estimated that the contribution of *P. margaritifera* to this stock would be low (0.5 to 5%) compared to wild species and in particular to *P. maculata* (65 - 91%). This suggests that high bivalve larvae concentration in the lagoon is not drastically modified by pearl oyster farming, despite 10% of the lagoon area dedicated to this activity. However, Thomas et al. prediction was based on experimental spat collectors immersed in the central part of the lagoon (close to stations 3 and 9) where the influence of outside oceanic water through the pass is the more important and where the pearl farming activity is the less intensive. Even with likely more than a few percent of farmed oysters, the relative abundance of bivalve larvae in the Ahe plankton is probably due to the importance of wild populations. The requirement to know the exact status of the wild population of bivalve has been pointed out by several of the study achieved in Ahe (Thomas et al., this issue, a). This will be a priority in subsequent studies.

The dominance of bivalve larvae also suggests an imbalance at the bottom of the trophic pyramid, resulting in a “bottleneck” between the second (primary consumers) and third (secondary consumers) trophic levels. According to Margalef (1968), this imbalance may be related to (1) food competition between bivalve larvae and the other nanoparticle feeders and (2) dominant prey (bivalve larvae) having shells and, therefore, being difficult to consume. This second point is supported by the absence of correlation between bivalve larvae and predator, while positive correlations were found between other zooplankton prey (pico feeders and other nano feeders) and predators (see Table 3). However, further investigation on the structure and functioning of the trophic network is required to explore these hypotheses

4.3. Spatio-temporal distribution of zooplankton

As for the aforementioned microorganisms, **w**ind-driven water circulation may partly explain the spatiotemporal variations of zooplankton in the lagoon. It is generally accepted that, in closed or semi-closed shallow aquatic ecosystems, the wind effect on the water column mixing, combined with vertical migration (and distribution) of organisms exert a very significant influence on the zooplankton horizontal distribution (Boltovskoy et al., 1984), including in coral reef systems (Alldredge and King, 2009). Besides, in coastal marine ecosystems wind-driven circulation and the behavior of larvae of individual bivalve species have been shown to interact to produce patches of high larval abundance (Ma et al., 2006).

In this study, during the windy period (October 2008) the total abundance and biomass were lower at stations 1-3 (on the western zone) than at stations 9-11 (eastward zone). This increase was mainly due to the accumulation of bivalve larvae (Fig. 4) with copepods being relatively more abundant at stations 1-3. Such a pattern is consistent with the observations by Carleton and Doherty (1998) in another atoll of the Tuamotu Archipelago (Taiaro) where zooplankton formed distinctive, consistently different assemblages in the windward and leeward areas during the windy period. They argued that this spatial pattern probably resulted from the combination of hydrodynamic circulation within the lagoon and species specific behavior. Water circulation in closed atoll lagoons is typically dominated by wind-driven circulation with surface water moving downwind, balanced by a compensatory reverse flow near the bottom resulting in upwelling at the windward margin and downwelling at the leeward side (Michel, 1969; Atkinson et al., 1981, Dumas et al., this issue). Actively vertical migrating species should, therefore, accumulate in the downwelling zone, owing to their distribution on the surface at night, while deep-living species should prevail in the upwelling zone. According to this pattern the higher relative abundance of some copepods (*Undinula vulgaris*, *Paracalanus/Clausocalanus* spp., *Acartia* sp and *Oithona* spp.) at the westward stations (stations 1-3) than at eastward stations (stations 9-11) in October 2008 (see Table 1), could be explained by their nocturnal migration to the upper water layer.

Calanoid copepods such as *Acartia, Paracalanus* and *Clausocalanus* (Pagano et al, 1993; Cuker and Watson, 2002; Lo et al, 2004) as well as small *Oithona* species (Tanimura et al., 2008) have been shown to exhibit typical diel vertical migrations (DVM) in contrasting habitats. We found no such evidence (nor contrary evidence) for *Undinula vulgaris* in the literature, but, over a 24-h sampling survey at a coastal station (5 m depth) near the field laboratory (east side of the atoll), we observed high nocturnal abundance and quasi diurnal absence of this species (unpublished data), suggesting a strong migratory behavior and possible DVM in the Ahe lagoon. On the other hand, high abundance of bivalve larvae at the eastward stations (stations 9-11) could be partly explained by their permanent concentration in the deep layers (20 - 30 m) as observed by Thomas et al., (this issue, a). These authors observed in 2007-2008 a similar large-scale distribution pattern with high concentration of bivalve larvae in the eastern part by windy conditions. They suggested that the deep vertical distribution of the larvae could explain their horizontal distribution, the larvae being passively transported by the overturning upwind deep current leading to high larval concentration along

the eastern reef rim. The high transport potential for larvae observed by Thomas et al. (this issue, a) and the modeling study performed by Thomas et al. (this issue, b) has confirmed the existence of this circulation.

During the light wind period (May 2008) the central area (stations 3 and 9) was characterized by lower zooplankton biomass and abundance and lower percentages of meroplankton and bivalve larvae than at the coastal stations (stations 1 and 11). These differences can be explained by the tide-driven flush going through the pass, creating a jet-like circulation in the central area, according to the 3D hydrodynamical model by Dumas et al. (this issue). The resulting higher oceanic influence in the central part of the lagoon probably explains the higher relative abundance of typical oceanic zooplankton populations such as salps and appendicularians at station 3 and 9 compared to stations 1 and 11 (see Table 1). Hamner et al. (2007) also observed tidal export-import phenomena leading to changes of zooplankton community in a coral reef system (Palau). On the other hand, higher percentage of bivalve larvae at station 1 and 11 compared to stations 3 and 9 could reflect a stronger influence of pearl oyster farming at a period where low wind-driven overturning circulation limits larval dispersion over the lagoon.

4.4. Relationships between zooplankton and environmental and trophic variables

Our study revealed clear differences in zooplankton community between the different sampling periods, probably explained by either abiotic or biotic variables (see Co-inertia analysis, Fig 6). During the dry season survey (May 2008) characterized by high salinity (>36.8) and autotrophic-dominant trophic status (higher abundance of PNF and bacteria), the zooplankton community was mainly characterized by *Candacia* spp., *Labidocera* sp., *Oithona plumifera* and salps. During the other periods (October 2008 and February 2009), characterized by lower salinity (<36.6) and heterotrophic-dominant trophic status (higher abundance of HNF), the community was mainly characterized by harpacticoid (*Microsetella sp.*, *Tisbe sp.* and undetermined genera) and cyclopid (*Oncaea sp.*) copepods, medusae, Annelid and Cirriped larvae. Salinity and trophic status, therefore, appeared to be important causes explaining the time-variations of the zooplankton community.

Total zooplankton abundance was positively correlated with temperature, mainly due to the highest abundance recorded in February during the warmest period. Zooplankton composition was also dependent on temperature as shown by the multivariate analysis with the colder (October 2008) and the warmer (February 2009) surveys opposed on the second axis. The February 2009 survey was characterized by several rare zooplankton taxa such as Ctenophores, *Lucifer*, isopods, water mites and Cirriped and Actinotroch larvae. Alvarez-Cadena et al. (2009) also showed clear distinction between the dry season (November to May), and the wet season (June to October) for the composition and abundance of zooplankton in a coral reef lagoon, in relation with variations of similar abiotic factors (temperature and salinity).

The clearly higher zooplankton abundance and biomass at the coastal stations (1 and 11) than at the central ones (3 and 9) during the light wind period (May), (see Fig 5 and discussion above), can be related to concurrent higher phytoplankton and microheterotrophic biomass (see Fig. 4). Furthermore, we also observed a significant correlation between Chl *a* and zooplankton abundance (r=0.75, p=0.005). These results suggest a bottom-up control of zooplankton in the lagoon. This type of control is relatively common in oligotrophic ecosystems, such as atoll lagoons, where the primary production is limited by low nutrient levels and where phytoplankton biomass availability is a limiting factor for the production of the upper trophic levels (Calbet et al., 1996). In the Ahe lagoon, the bulk of phytoplankton consists of picophytoplankton which cannot be directly consumed by most zooplankton taxa including the most abundant ones, such as bivalve larvae (Doroudi and Southgate, 2003). To fulfill their energy needs, these organisms had to consume nano- or micro-particles such as

organic detritus, transparent exopolymeres (TEP) which were abundant during this study (Durieux, pers. com.) and heterotrophic organisms produced trough the microbial loop.

The importance of detritus as food for lagoon zooplankton was shown by Gerber and Marshall (1974) in Eniwetok Lagoon (Marshall Islands), and by Le Borgne et al (1989) in Tikehau Atoll lagoon. The use of TEP as a food source for zooplankton was suggested by Ling and Alldredge (2003), although other works have shown an inhibiting effect (Dutz et al., 2005). The importance of the microbial loop for the production of the upper trophic levels in atoll lagoons has been shown in previous studies. Sakka et al. (2002) showed that protozoa played a key role in the Takapoto atoll by exerting strong grazing pressure on picoplankton and were themselves a major food source for metazoan zooplankton. In the same lagoon, Loret et al. (2000) showed that hetero/mixotrophic protists processed the picoplanktonic resource rapidly and efficiently for filter-feeders, particularly pearl oysters. In the Ahe lagoon, the importance of the microbial loop is supported by the study of Michotey et al (this issue) showing spatiotemporal pervasiveness for heterotrophic groups such as *Marinovum*, *Flavobacteria* and *Erytrobacter.* The trophic link between metazooplankton and the microbial loop is suggested by our positive correlations between ciliates and total zooplankton ($r=0.82$, $p=0.01$) and by the PCA for the functional groups (Fig. 7) which showed clear links between HNF and nano particle feeders, as well as between ciliates and bivalve larvae. It is also supported by the Co-inertia analysis (Fig 6) which showed a clear opposition between the May 2008 survey, where the herbivory components of the food chain prevailed with the large numbers of PNF and the presence of salps, and the surveys in October 2008 and February 2009 where the predominance of the heterotrophic microbial components (higher abundance of HNF) was associated with a zooplankton community characterized by harpacticoid (*Microsetella* sp., *Tisbe* sp. and undetermined genera) and cyclopid (*Oncaea* sp.) copepods and by medusa, Annelid and Cirriped larvae. The association of salps with PNF and bacteria may be linked to their ability to graze not only on 2 to 200 µm phytoplankton but also on 0.5 to 2 µm free-living bacteria and picophytoplankton, owing to their mucus net filtering structures (Riisgard and Larsen, 2010). On the other hand, the association of harpacticoids and cyclopids with the heterotrophic network may be linked to their ability to utilize a variety of food materials including detritus, organic flocs, fecal pellets and protists (Lewis et al., 1998; Metz, 1998).

5. Conclusion

Our results showed the predominance of meroplankton and bivalve larvae in Ahe as compared to other coral reef and atoll lagoons. while the dominance of bivalve larvae suggests potentially major community change arising from aquaculture activities (pearl oyster farming), it is probably mainly due to the importance of wild populations. Our study also suggests that tide-flushing and wind driven circulation of the lagoon, as evidenced in the study by Dumas et al. (this issue), plays an important role in shaping the time and space distribution of the zooplankton. Salinity, temperature and trophic status (autotrophic *vs* heterotrophic) seem to be the main forcing variables for the abundance and composition of the metazooplankton community. The preponderance of picophytoplankton within the phytoplankton community and the abundance of nanoparticle feeders are indirect evidence of the importance of the microbial loop in Ahe lagoon.

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Tables

Table 1 : Mean values between sampling dates of taxa numbers, total zooplankton abundance and percentage contribution of taxa in the four sampled stations during the three surveys: May 2008 (M1, M3, M9, M11), October 2008 (O1, O3, O9, O11) and February 2009 (F1, F3, F9 and F11). The symbols of the taxa for the multivariate analyses are indicated in the second column.

		May 2008				**October 2008**				**February 2009**			
		M1	M3	M9	M11	O1	O3	O9	O11	F1	F3	F9	F11
COPEPODA %		**24.5**	**44.6**	**39.2**	**35.2**	**67.9**	**56.9**	**32.4**	**33.5**	**34.2**	**32.9**	**39.7**	**27.9**
nauplii	NAU	12.28	11.92	12.37	11.37	27.02	23.50	13.09	17.80	7.12	11.68	16.83	12.45
unidentified	COPI	0.37	0.04	0.09	0.08	0.22	0.45	0.68	0.55	1.53	2.10	1.42	0.73
Paracalanus/Clausocalanus	par	3.74	8.18	7.92	9.72	8.10	7.77	4.96	3.58	7.20	5.57	6.67	8.14
Acartia spp.	Aca	0.34	0.09	0.14	0.09	1.79	0.26			0.41	0.07	0.07	0.16
Undinula vulgaris	Und	0.14	0.21	0.24	0.08	0.14	0.25	0.10	0.04	0.05	0.07	0.20	0.32
Candacia pachydactyla	Cpa		<0.01	<0.01	0.01								
candacia varicans	Cva		0.01										
Calanopia minor	Cmi	0.06	<0.01	0.04	0.04	0.17	0.34	0.28	0.10	1.38	1.48	1.30	1.46
Labidocera sp.	Lab		<0.01	0.01				<0.01					
Corycaeus	Cor	0.08	0.92	1.41	0.29	0.33	0.25	0.90	1.18	0.38	0.64	0.90	0.79
Oncaea	Onc			0.02				<0.01		0.07	0.12	0.03	0.01
Oithona sp.	Oit	7.51	23.17	16.76	12.98	29.06	23.78	12.23	9.90	15.99	10.87	12.18	3.57
Oithona plumifera	Opl		0.03	0.23	0.55								
Sapphirinidae	Sap		0.01									<0.01	0.01
Microsetella sp.	Mic	<0.01	<0.01	<0.01		0.02	0.10	0.21	0.05	0.01	0.12	0.06	0.12
Tisbe sp.	Tis					0.52	0.09		0.14	0.02	0.07	0.03	0.04
Harpacticoid unidentified	HAR			0.01							<0.01	0.01	0.04
Tisbe sp.	Tis					0.52	0.09		0.14	0.02	0.07	0.03	0.04
OTHER HOLOPLANKTON %		**1.1**	**4.9**	**5.0**	**1.7**	**7.7**	**8.6**	**5.3**	**4.4**	**12.0**	**21.2**	**9.4**	**10.7**
Appendicularians	APP		2.02	0.92	0.73	2.86	4.07	2.24	1.77	1.69	5.08	2.73	2.80
Chaetognaths	CHA	0.84	0.68	1.28	0.72	3.28	1.59	1.19	1.30	1.02	1.74	1.35	2.55
Pteropods	PTE	0.13	0.55	0.17	0.22	1.27	2.92	1.87	1.34	9.11	14.34	5.27	5.18
Isopods	ISO	0.02			0.01							<0.01	
Ostracods	OST	0.01	0.10	0.11	0.02		0.03	0.02	0.03	0.04	<0.01	0.02	0.06
Salps	SAL	0.09	1.47	2.49	<0.01	0.01	<0.01		<0.01		<0.01		
Medusae	MED					0.03	<0.01			<0.01			
Lucifer	LEU	<0.01				<0.01		<0.01		0.03	<0.01	<0.01	0.02
Amphipoda	AMP	0.01	0.03	0.08	0.03					0.01	0.02	0.03	0.06
Ctenophora	CTE	0.01		<0.01								<0.01	
Water mites	WMI	<0.01											
Foraminifera	FOR		<0.01	<0.01									
Protozoans	PRO					0.25		0.01		0.07	0.02		0.06
LARVA (MEROPLANKTON) %		**73.0**	**50.5**	**55.7**	**63.0**	**24.9**	**34.6**	**62.2**	**62.2**	**53.9**	**46.0**	**50.9**	**61.4**
Gastropod	LGA	16.49	7.54	7.47	16.94	11.86	9.13	8.30	11.20	19.81	12.63	10.72	11.56
Bivalve	LBI	56.01	42.85	47.78	45.87	11.47	19.26	52.57	50.41	33.71	32.92	39.64	49.45
Euphausid	LEU	0.02				0.15	0.02	<0.01		0.01	<0.01	<0.01	0.01
Decapod	LDE	0.31	0.08	0.08	0.03	0.23	0.03	0.04	0.06	0.09	0.02	0.04	0.09
Zoea	LZO	<0.01	<0.01	0.01	0.02	0.19	0.01	0.03	0.01	0.03	0.02	0.01	0.01
Fish	LFI	0.06	0.04	0.02	0.03	0.11	0.01		0.00	0.02	0.01	0.04	0.05
Polychaete	LPY	0.01	<0.01	0.07	0.01	0.09	0.08	0.05	0.06	0.11	0.07	0.03	0.09
Echinoderm	LEC	0.07	0.03	0.29	0.14	0.83	5.67	1.17	0.44	0.05	0.24	0.40	0.17
Actinotroch	LAC	<0.01									<0.01		
Cirriped	LCI									0.01	0.05		
Asteroid	LAS					0.02	0.39	0.06	0.03	0.01	0.04	0.01	0.01
TOTAL ABUNDANCE (ind. m-3)		**23324**	**5830**	**6501**	**21222**	**5058**	**9098**	**18451**	**17134**	**27173**	**17660**	**13055**	**17795**
Nb Taxa		28	28	29	24	26	25	24	22	29	31	30	29

Table 2 : Pearson's correlation coefficients between zooplankton biomass (total and by size classes) and abundance (total and for the main groups) and environmental and trophic factors. Significant values after Bonferroni correction for multiple comparison (p<0.005) are in bold characters. N=12. Proc = *Prochlorococcus sp.*, Syn = *Synechococcus sp,* Pico = picoeukaryotes, PNF = Pigmented (autotrophic) nanoflagellates, Bact = bacteria, HNF = heterotrophic nanoflagellates, Cil = ciliates.

	Biomass				Abundance				
	Total	>500 µm	200-500 µm	80-200 µm	Total	copepods	Others	Mero plankton	Bivalve larvae
T	0.444	0.412	0.430	0.456	**0.757**	0.057	0.423	0.317	0.255
	p=0.148	p=0.183	p=0.163	p=0.136	**p=0.005**	p=0.861	p=0.171	p=0.315	p=0.424
S	-0.317	-0.492	-0.370	-0.023	-0.165	-0.442	**-0.862**	-0.094	-0.003
	p=0.316	p=0.105	p=0.236	p=0.942	p=0.608	p=0.150	**p=0.000**	p=0.771	p=0.992
Chl tot	0.660	0.601	0.540	0.667	**0.754**	0.469	0.348	0.622	0.609
	p=0.019	p=0.039	p=0.070	p=0.018	**p=0.005**	p=0.124	p=0.268	p=0.031	p=0.036
Chl <2µm	0.676	0.591	0.578	0.705	**0.802**	0.441	0.352	0.628	0.602
	p=0.016	p=0.043	p=0.049	p=0.010	**p=0.002**	p=0.151	p=0.261	p=0.029	p=0.038
Chl>2µm	0.471	0.513	0.299	0.410	0.452	0.455	0.247	0.483	0.513
	p=0.122	p=0.088	p=0.345	p=0.185	p=0.140	p=0.137	p=0.439	p=0.112	p=0.088
Proc	-0.049	-0.049	0.055	-0.080	-0.403	0.212	0.174	0.091	0.077
	p=0.880	p=0.879	p=0.866	p=0.804	p=0.194	p=0.507	p=0.589	p=0.779	p=0.812
Pico	0.555	0.638	0.505	0.412	0.704	0.244	0.689	0.330	0.271
	p=0.061	p=0.026	p=0.094	p=0.184	p=0.011	p=0.445	p=0.013	p=0.294	p=0.395
Syn	0.387	0.502	0.437	0.086	0.081	0.617	0.628	0.125	0.059
	p=0.215	p=0.097	p=0.156	p=0.791	p=0.803	p=0.032	p=0.029	p=0.699	p=0.855
PNF	-0.129	-0.296	-0.200	0.152	0.157	-0.408	-0.662	0.037	0.099
	p=0.690	p=0.351	p=0.533	p=0.637	p=0.625	p=0.189	p=0.019	p=0.908	p=0.759
Bact	-0.353	-0.523	-0.398	-0.058	-0.225	-0.389	**-0.836**	-0.085	-0.003
	p=0.261	p=0.081	p=0.200	p=0.857	p=0.483	p=0.211	**p=0.001**	p=0.793	p=0.992
HNF	0.328	0.463	0.356	0.052	0.006	0.565	0.677	0.160	0.119
	p=0.298	p=0.130	p=0.255	p=0.871	p=0.986	p=0.056	p=0.016	p=0.619	p=0.712
Cil	0.563	0.447	0.505	0.665	**0.821**	0.152	0.234	0.536	0.507
	p=0.057	p=0.146	p=0.094	p=0.018	**p=0.001**	p=0.638	p=0.463	p=0.073	p=0.093

Table 3 : Pearson's correlation coefficients between the different trophic groups: picophytoplankton (= sum of *Prochlorococcus sp.*, *Synechococcus sp,* and picoeukaryotes), pigmented (autotrophic) nanoflagellates (PNF), bacteria (Bact), heterotrophic nanoflagellates (HNF), ciliates.(Cil), predators (= sum of Chaetognaths, medusae, ctenophores, *Labidocera* spp, *Candacia* spp, *Corycaeus* spp, *Oncaea* spp and fish larvae), picoparticle feeders (pico F = sum of salps and appendicularians), bivalves and other nanoparticle feeders (nano F = other metazooplankton organisms). Significant values after Bonferroni correction for multiple comparison (p<0.006) are in bold characters. N=12.

	picophyto	PNF	Bact	HNF	Cil	Predators	nano F	pico F
PNF	**-0.889**							
	p=0.000							
Bact	**-0.754**	**0.848**						
	p=0.005	**p=0.000**						
HNF	**0.892**	**-0.944**	**-0.837**					
	p=0.000	**p=0.000**	**p=0.001**					
Cil	-0.329	0.453	-0.042	-0.298				
	p=0.296	p=0.139	p=0.897	p=0.348				
Predators	**0.771**	**-0.665**	**-0.802**	**0.787**	0.209			
	p=0.003	**p=0.018**	**p=0.002**	**p=0.002**	p=0.514			
nano F	0.644	-0.429	-0.668	0.540	0.444	**0.871**		
	p=0.024	p=0.164	p=0.017	p=0.070	p=0.148	**p=0.000**		
pico F	0.683	-0.584	-0.689	0.575	0.163	**0.739**	**0.808**	
	p=0.014	p=0.046	p=0.013	p=0.051	p=0.613	**p=0.006**	**p=0.001**	
Bivalves	0.165	0.099	-0.003	0.119	0.507	0.461	0.498	0.298
	p=0.608	p=0.759	p=0.992	p=0.712	p=0.093	p=0.131	p=0.099	p=0.347

Figures

Figure 1 : Left: Location of Ahe (sampling sites) and Takaroa (meteo station) atolls. Right: Positions of the sampling stations in the Ahe lagoon.

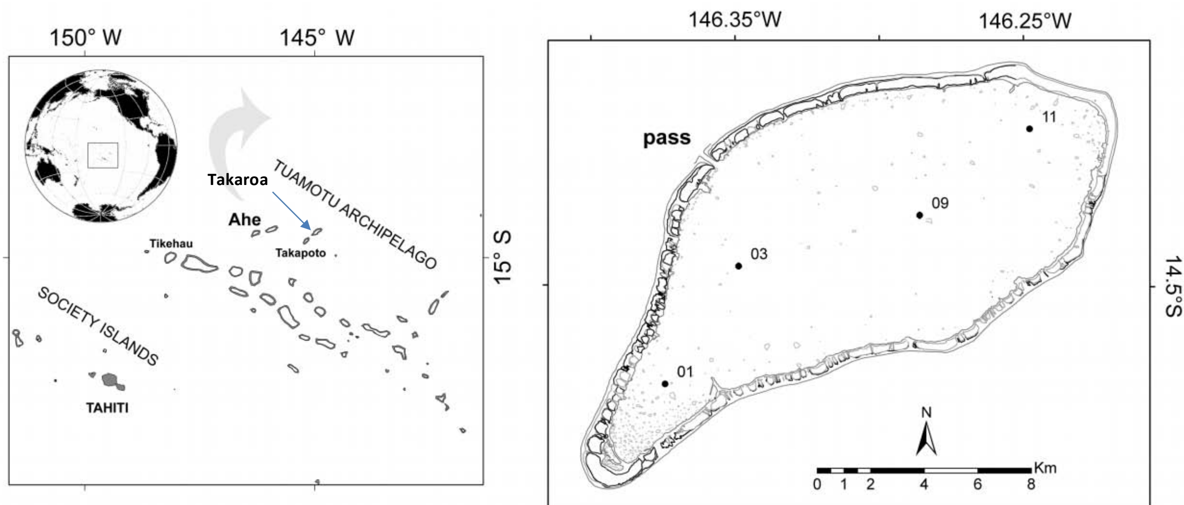

Figure 2 : Average values of (a) rainfalls and air temperature and (b) wind speed and direction recorded at Takaroa meteorological station. Sampling periods are indicated with arrows

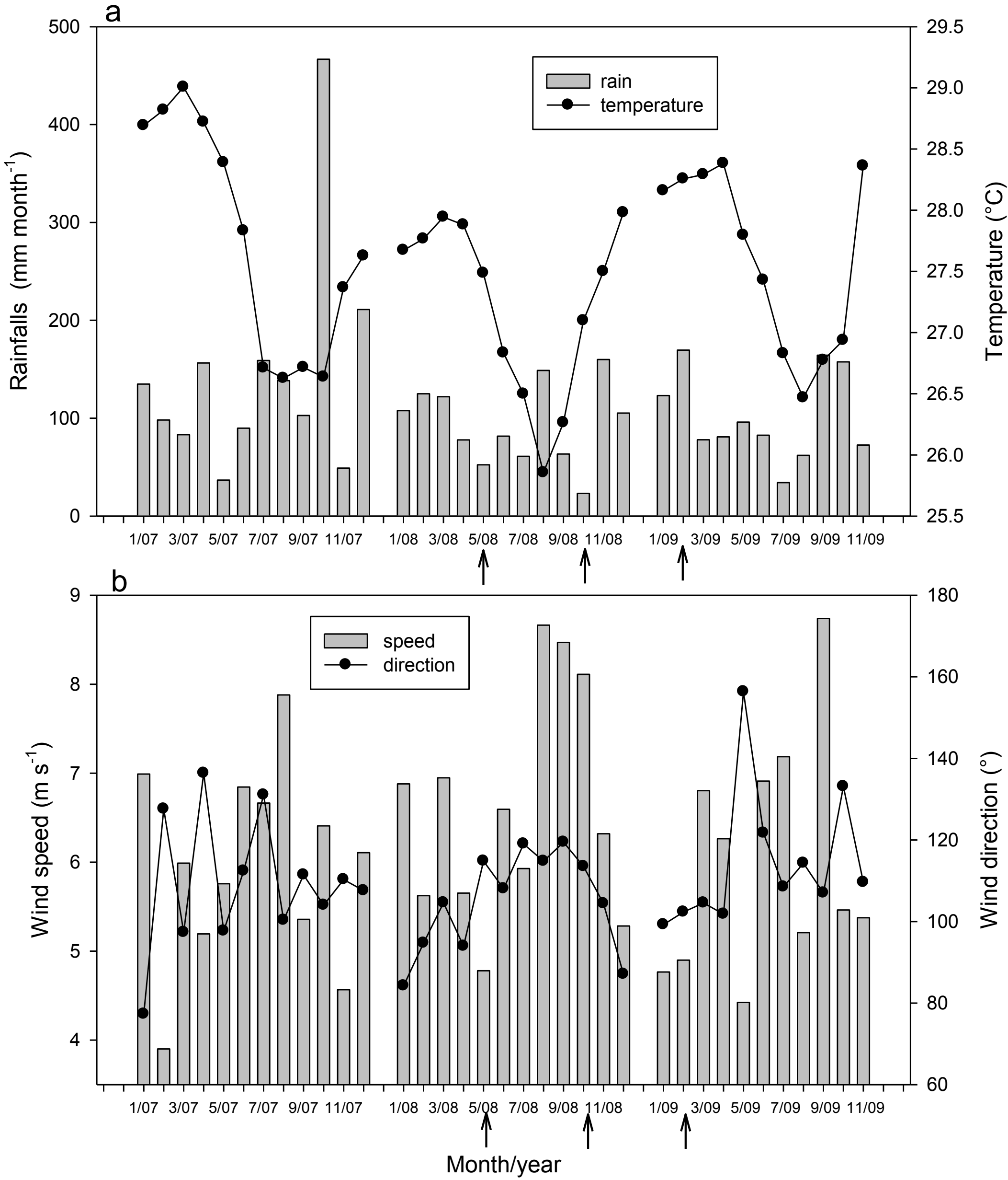

Figure 3 : Mean water column (between sampling dates) temperature and salinity at the four sampled stations (1, 3, 9, 11) during the three surveys: May 2008 (M1, M3, M9, M11), October 2008 (O1, O3, O9, O11) and February 2009 (F1, F3, F9, F11).

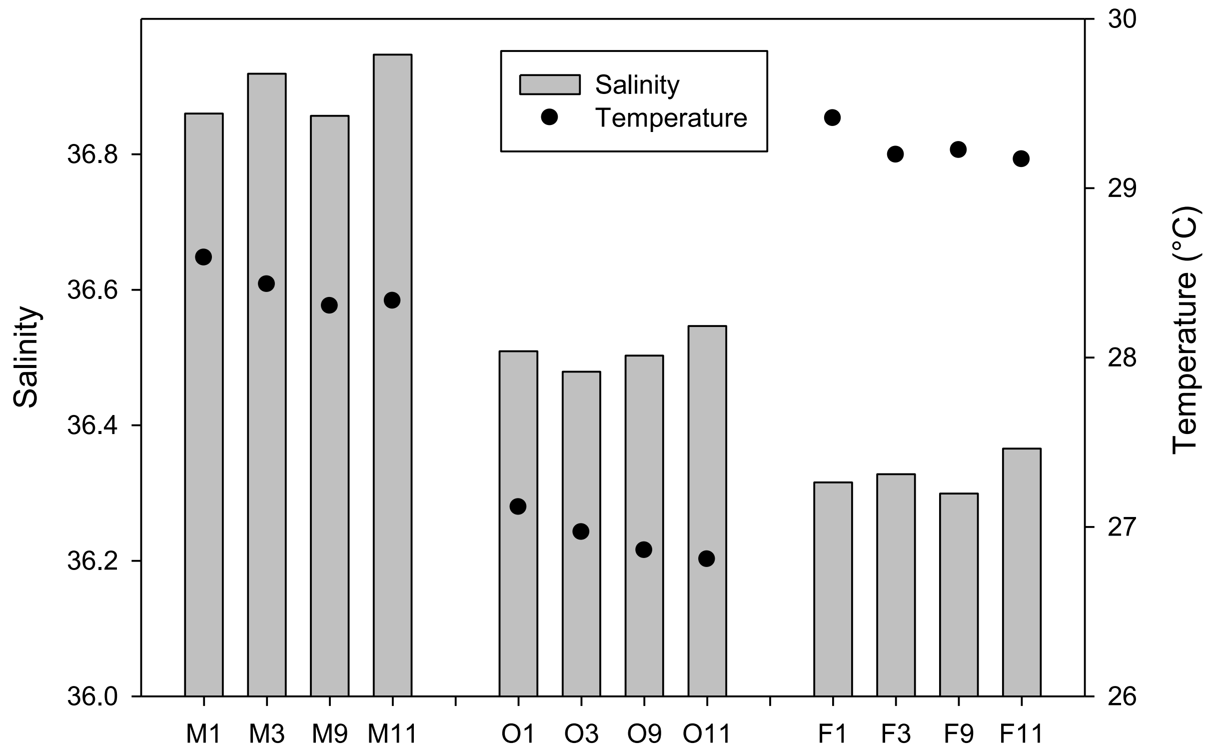

Figure 4 : Mean water column values (between sampling dates) of (a) Chlorophyll a (two size-fractions), (b) autotrophic microorganisms (picoeukaryotes, Pico, Synechococcus, Syn, and pigmented nano flagellates, PNF) and (c) heterotrophic migoorganisms (bacteria, Bact, heterotrophic nanoflagellates, HNF and ciliates, Cil) at the four sampled stations (1, 3, 9, 11) during the three surveys: May 2008 (M1, M3, M9, M11), October 2008 (O1, O3, O9, O11) and February 2009 (F1, F3, F9, F11).

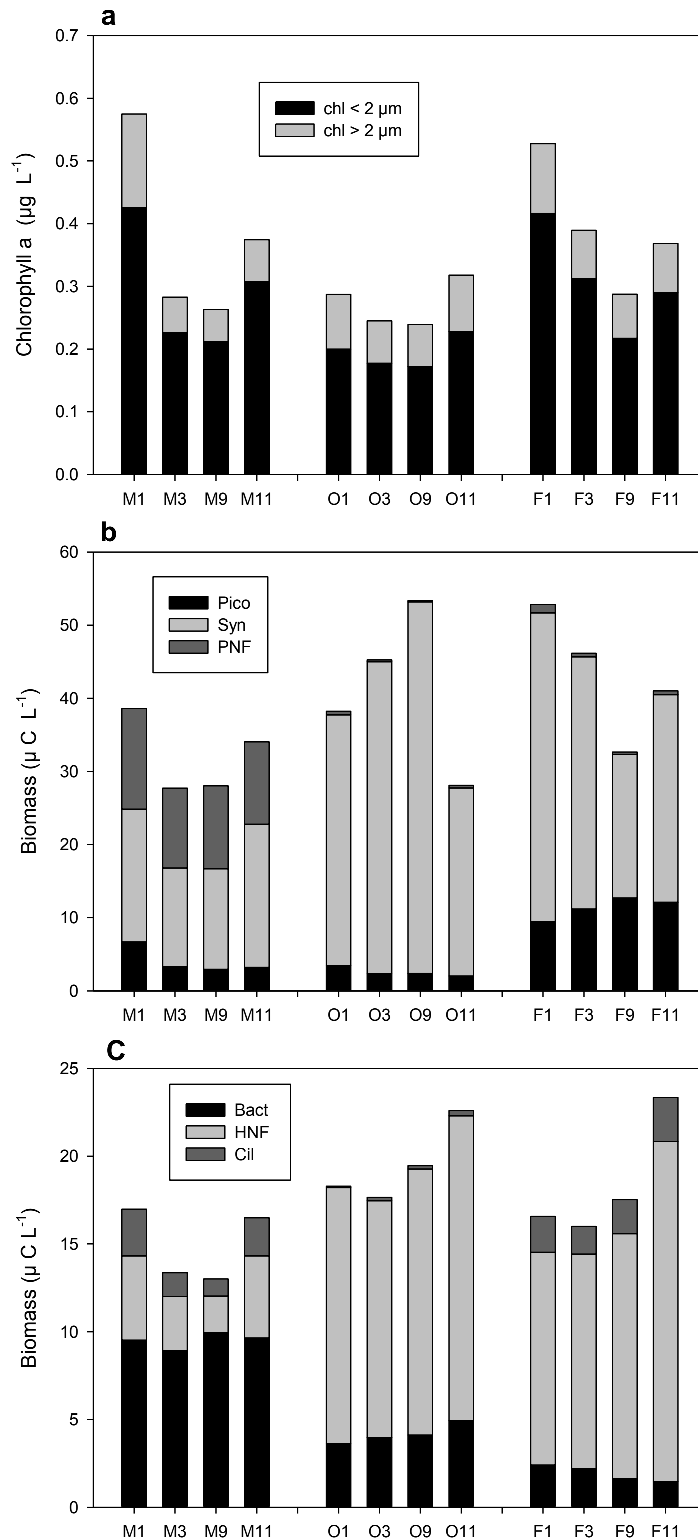

Figure 5 : Mean values (between sampling dates) of (a) abundance of the main zooplankton groups (copepods, other holoplankon and larvae) and (b) zooplankton biomass (by size-classes) as expressed in mg Dry weight (DW) per cubic meter at the four sampled stations (1, 3, 9, 11) during the three surveys: May 2008 (M1, M3, M9, M11), October 2008 (O1, O3, O9, O11) and February 2009 (F1, F3, F9, F11).

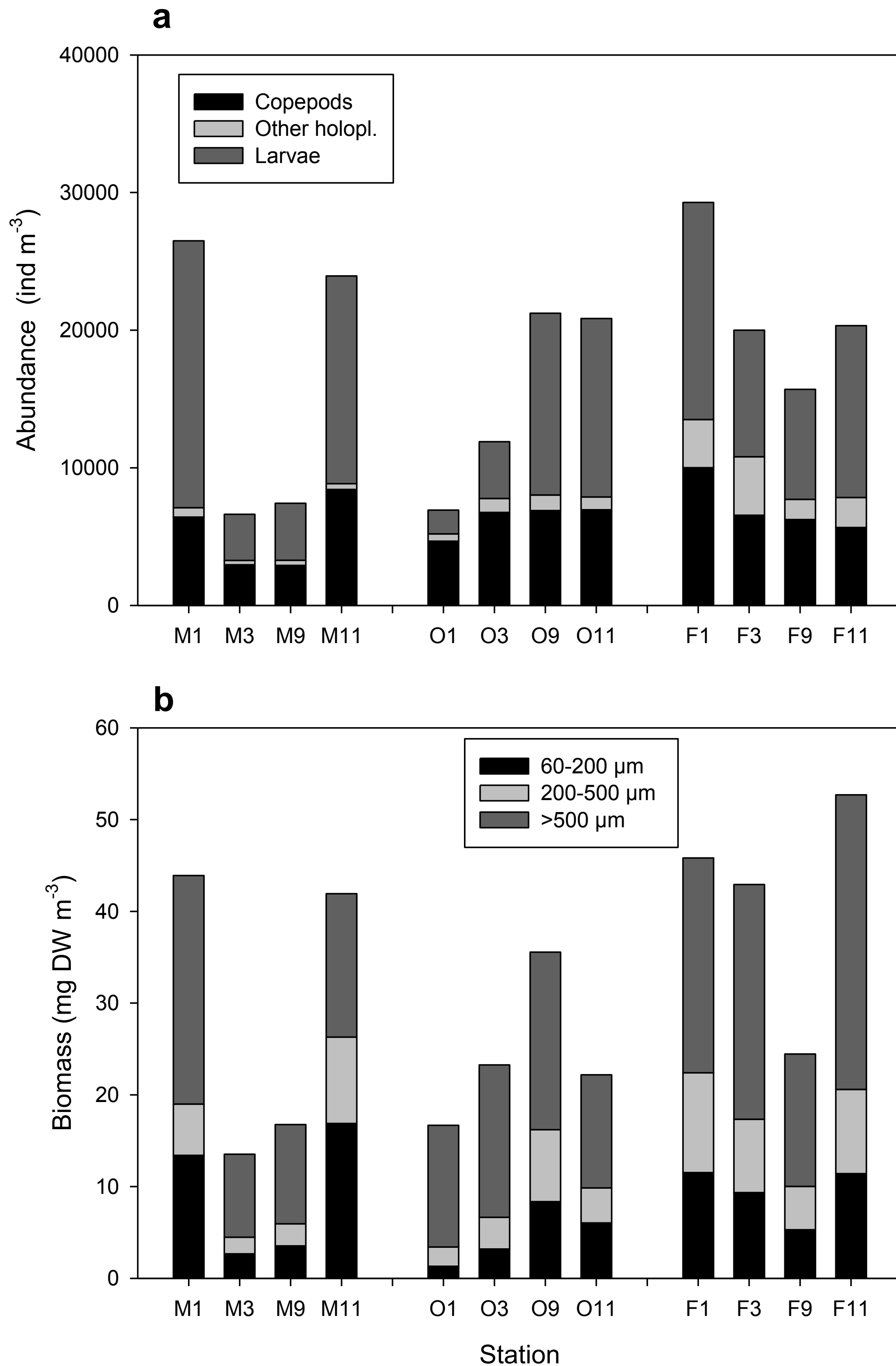

Figure 6 : Co-inertia analysis plots of (a) the environmental variables and (a) the stations in the "Environment" system and plots of (c) the taxa and (d) the stations in the "Zooplankton" system. Abbreviations as in Tables 1 and 2.

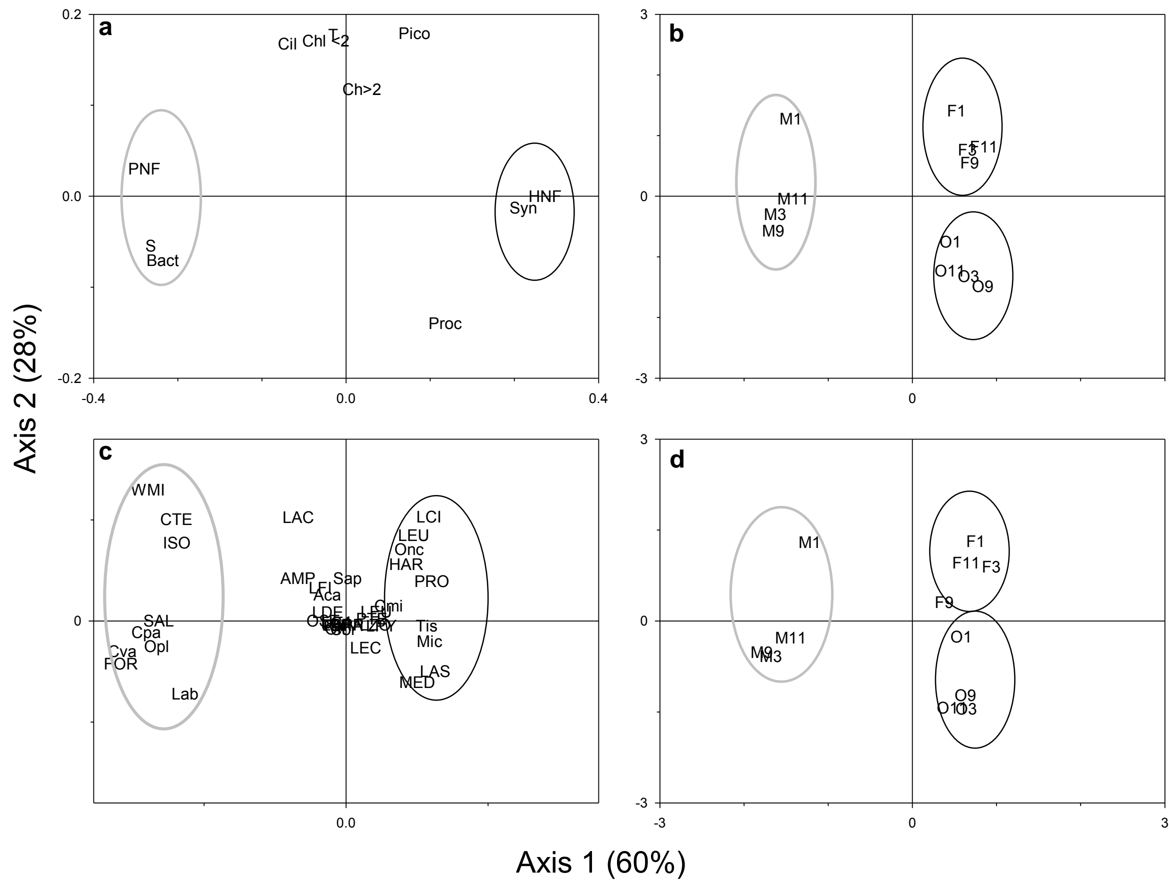

Figure 7 : Principal Component Analysis (PCA) of the trophic functional groups: plots of (a) the trophic variables and (b) the stations on the first factorial plane.