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The plankton food web of the Bizerte Lagoon (South-western Mediterranean): II. Carbon steady-state modelling using inverse analysis

Boutheïna Grami [a,b,*], Nathalie Niquil [b], Asma Sakka Hlaili [a], Michel Gosselin [c], Dominique Hamel [c], Hassine Hadj Mabrouk [a]

[a] Laboratoire de cytologie végétale et de phytoplanctonologie, Faculté des Sciences de Bizerte, 7021 Zarzouna, Bizerte, Tunisia
[b] Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, UMR 6217, Université de La Rochelle, Av. Michel Crépeau, 17042 La Rochelle Cedex 1, France
[c] Institut des Sciences de la Mer de Rimouski (ISMER), Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

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ABSTRACT

A steady-state model of the planktonic food web of the Bizerte Lagoon (Tunisia, South-western Mediterranean) was developed to characterize its structure and functioning through four stations: MA under urban discharge, MB impacted by industrial input, MJ located at proximity of shellfish farming and R in the central area of the lagoon. Carbon stocks of eight chosen compartments were determined and flows were assigned for each one from field data. Missing flow values were calculated by inverse analysis for each station. Network analysis was applied to the resulting food web models to characterize their properties. These analyses mainly showed similarity among stations concerning (1) a high primary production of phytoplankton which was dominated by >10 μm cells (i.e. diatoms); (2) important herbivory against detritivory in stations MA and MJ; (3) major role of detritivory in stations MB and R; (4) efficiency of microbial link in transferring carbon for higher trophic level; (5) efficiency of microzooplankton as a trophic link between detritus, dissolved organic carbon, autotrophs and mesozooplankton; (6) important recycling of carbon leading to conclude about an immature state of the ecosystem. Differences between the functioning of microbial food webs in the lagoon are mainly due to the location of stations. The proximity of station MB to inland and industrial discharges affected its productivity and made it the least productive station. Water circulation into the lagoon made pollutant concentrate into the south and the western sections which seemed to affect the planktonic food web, since the values of productivity reported for stations MB and R were lower than those calculated for the others stations.

1. Introduction

The Mediterranean Sea is known to be an oligotrophic ecosystem characterized by a microbially dominated food web (Fogg, 1995). This is the case of Thau Lagoon web (Bec et al., 2005), Mallorca coastline (Sintes et al., 2004), Lake Kinneret (Stone et al., 1993) and the Bay of Tunis (Souissi et al., 2000). Other Mediterranean coasts showed different trophic status. The Adriatic Sea impacted by inputs from the Po River is known to be mesotrophic (Crispi et al., 2001) with different trophic food web. A study driven in the Gulf of Trieste showed that the microbial food webs are the trophic basis for the whole community coastal system, (Umani and Beran, 2003; Berglund et al., 2005) while in the Varano Lagoon the classical food web is more developed than the microbial one (Caroppo, 2000). The Aegean Sea, impacted by discharges from the Black Sea is mostly eutrophic (Crispi et al., 2001) but the energy transfer is efficient through microbial food web (Isari et al., 2006). The Ligurian Sea, Villefranche Bay, shows a variation of the trophic character from oligotrophic (Lacroix and Nival, 1998) to mesotrophic (Selmer et al., 1993) and the food web is predominantly based on the microbial loop (Rassoulzadegan and Sheldon, 1986; Thingstad et al., 1998). In the Mar Menor, Gilabert (2001) statuted the importance of the microbial loop.

These conclusions were made based on the composition and the variation of the different living and non-living planktonic components. Within the past decades, biological oceanographers realized that studies of plankton biomass and specific composition were not sufficient enough to understand the structure and functioning of marine plankton systems. As a consequence, the interaction

* Corresponding author. Laboratoire de cytologie végétale et de phytoplanctonologie, Faculté des Sciences de Bizerte, 7021 Zarzouna, Bizerte, Tunisia.
E-mail address: grami_boutheina@yahoo.fr (B. Grami).

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between the various planktonic components became of increasing interest.

Furthermore, data from studies of food web processes were integrated into models that consider the planktonic ecosystem as a whole rather its components separately. These models provided a consistent description of trophic interactions between various functional groups of the planktonic ecosystem. There were numerical food web models (Steel and Frost, 1977; Steel and Henderson, 1981), compartmental model (Platt et al., 1981) and flow analysis models (Fasham, 1985). All of them required good knowledge of the ecological processes occurring in the concerned study areas. The crucial problem of these models is that most of the flows, between compartments, are difficult to measure, confronting the researchers to an incomplete data set. In order to resolve this, Vézina and Platt (1988) applied the analytical method known as inverse analysis to planktonic food webs. The inverse method has been used extensively in the analysis of physical systems (Parker, 1977; Wunsch, 1978; Bolin et al., 1983). In fact, it's an optimization technique which provides a complete steady-state model of the food web by estimating the unknown flows, using known information to constrain the biological processes and parsimony principle.

Since inverse method provided a powerful tool to estimate ecosystem flows, it has been used to describe carbon flows of a wide range of environments such as the British coast (Vézina and Platt, 1988), the Southern California coast (Jackson and Eldridge, 1992; Eldridge and Jackson, 1993), the Baltic Sea (Donali et al., 1999), the Michigan Lake (Vézina and Pace, 1994), the Takapoto Atoll Lagoon, French Polynesia (Niquil et al., 1998, 1999), the North Pacific (Vézina and Savenkoff, 1999), the East Equatorial Pacific (Richardson et al., 2004), the Northern Gulf of St. Lawrence (Savenkoff et al., 2004), the Lake Biwa, Japan (Niquil et al., 2006) and the Bay of Biscay, France (Marquis et al., 2007).

The Bizerte Lagoon is experiencing different human impacts (urban, agricultural or industrial) and it supports intense fisheries and aquaculture farms. In this area, the various trophic compartments have generally been investigated separately [e.g. phytoplankton (Sakka Hlaili et al., 2006); protozooplankton (Sakka Hlaili et al., 2007); copepods (Hamdi et al., 2002)]. So, until now, the global functioning of the planktonic community as a whole, has been poorly studied in Bizerte Lagoon. During a study carried out in the lagoon (Sakka Hlaili et al., 2008), the standing carbon stocks of several trophic components (bacteria, phytoplankton, microzooplankton, mesozooplankton) and some carbon flows (phytoplankton and bacterial production, microzooplankton grazing) were estimated. The data were gathered into four stations (MA, MJ, MB and R) in summer, considered as the growing season in the lagoon (Sakka Hlaili et al., 2007). In the present study, we used these data and we measured the vertical flux of carbon. Then, we completed the lacking carbon flow values, by using the inverse analysis, in order to build up a model of the planktonic food web in the lagoon. Moreover, to analyse the full structure of all carbon pathways involved in this model, a network analysis was applied. This study, by using the two numerical approaches, is the first that characterizes the structure and the functioning of planktonic food web of the Bizerte Lagoon. The purpose of the present work is to provide answers to the following questions: how does the planktonic food web function in the Bizerte Lagoon? What are the main differences between stations in the Lagoon? How important is the primary productivity and does it provide enough carbon to higher trophic levels? How important the role of microzooplankton against mesozooplankton? What is the state of the lagoon in comparison to other marine systems in terms of productivity, trophic structure of the planktonic system, carbon transfer and eutrophication?

2. Material and methods

2.1. Study site

Bizerte Lagoon (37°8′–37°14′ N, 9°48′–9°56′ E; Fig. 1) is located on the northern coast of Tunisia. It has a surface area of 121.6 km^2 and maximum and mean depths of 12 and 8 m, respectively. The lagoon is connected to the Mediterranean Sea through a 7 km long, 300 m width and 12 m deep channel. Marine inflows are important in summer while freshwater is mainly supplied in winter (20 $Mm^3\,yr^{-1}$; Harzallah, 2002) from several surrounding rivers and the Lake Ichkeul. Tidal and wave forcing are negligible compared to that of the wind, which is the main factor controlling water circulation in the lagoon (Harzallah, 2003).

2.2. Sampling and water analyses

Sampling was carried out during summer 2004 at four stations (MA, MB, MJ and R; Fig. 1). Stations MA and MB are impacted by urban and industrial discharges, respectively. Station MJ is located at proximity of shellfish farming, while station R represented the lagoon central area. Water was collected at three depths, using an acid-washed 2.5 l water sampler PWS (Hydro-Bios), then (except water used for POC determination) pre-filtered through a 200 μm mesh screen and stored in isothermal containers until it was processed. Subsamples were taken to measure dissolved organic carbon (175 ml) and Chl *a* (1000 ml). Water samples (varied volume according to station, filtration stopped until ice-tea color was observed on the filter) for determination of particulate organic carbon (POC) were filtered on pre-combusted (at 450 °C, during 2 h) GF/F filters (21 mm) and analysed on a CHN elemental analyser (Perkin–Elmer 2400), as described in the JGOFS report (Knap et al., 1996). Other subsamples served to identify and/or enumerate bacteria (20 ml), picophytoplankton (20 ml), ≥2 μm phytoplankton (50–100 ml) and microzooplankton (100–200 ml). To determine composition and abundance of mesozooplankton, an horizontal net tow samples were taken at the surface using 200 μm screen mesh. Procedures are given in detail in Sakka Hlaili et al. (2008).

Two sediment traps (63 cm high, 6 cm internal diameter) were moored between 7 and 9 m depth in each station, depending on the station's depth, to estimate the sinking of particles. After 24 h, all traps were returned to the laboratory and stored at −5 °C for a night to let particles settle. The supernatant was then removed from each trap, and the bottom fraction was collected. For each station, bottom fractions of the two moored traps were mixed together. Subsamples were taken from the trapped material to determine total particulate organic carbon (POC) (see above). Subsamples were preserved in borated formol for enumeration and measure of fecal pellets under inverted microscope. Other subsamples, filtered through GF/F, served to measure chlorophyll *a* (Chl *a*) concentrations. Pigment concentrations were estimated after overnight dark extraction at 4 °C in 90% acetone, using the spectrophotometric method given by Parsons et al. (1984).

2.3. Incubations

Dilution experiments (Landry and Hassett, 1982) were carried out in each station to estimate growth rates of phytoplankton and bacteria as well as rates of microzooplankton grazing on them. The details of procedure and calculation are given in Sakka Hlaili et al. (2008).