

A new type of plankton food web functioning in coastal waters revealed by coupling Monte Carlo Markov Chain Linear Inverse method and Ecological Network Analysis

Marouan Meddeb^{a,b*}, Nathalie Niquil^c, Boutheïna Grami^{a,d}, Kaouther Mejri^{a,b}, Matilda Haraldsson^c, Aurélie Chaalali^{c,e,f}, Olivier Pringault^g, Asma Sakka Hlaili^{a,b}

Planktonic food web structure and functioning over seasons

To identify the dominant trophic pathway in marine environment, Sakka Hlaili et al. (2014) have proposed a specific ratio: the ratio of picophytoplankton net production to total phytoplankton net production (R7 ratio). This ratio was proposed by the authors to discriminate between herbivorous ($R7 \leq 0.1$), multivorous ($R7: 0.1-0.6$), and microbial food webs ($R7 \geq 0.6$). Based on this ratio, the spring food webs encountered in the Channel ($R7 = 0.1$) acted almost as a multivorous structure with a tendency towards herbivorous one, and the Bay ($R7 = 0.07$) functioned as herbivorous pathways. In both food webs, the high primary production was mainly dominated by large celled phytoplankton (mic). This agrees with earlier findings in the Bay and the Channel during spring, when several chain-forming diatoms dominated the microphytoplankton community (51–68%) (Meddeb et al., submitted). More specifically, the Bay and the Channel had the highest primary production during spring ($727-966 \text{ mg C m}^{-2} \text{ d}^{-1}$), dominated by microphytoplankton (Fig. 5). The stratification of the water column with high nutrient levels in the surface lever are favorable conditions for a microalgae bloom, which promotes the herbivore pathway. However, the primary production levels recorded here are lower than those found during this season in other productive regions, such as the Gulfs of Cadiz (SW Spain: $> 4500 \text{ mg C m}^{-2} \text{ d}^{-1}$) and of Biscay ($1507 \text{ mg C m}^{-2} \text{ d}^{-1}$) (Huertas et al., 2006; Marquis et al., 2007). Further, in both the herbivorous food webs, the protozooplankton, dominated by large heterotrophic/mixotrophic dinoflagellates (Meddeb et al., submitted), were the main grazers of phytoplankton (Table3), which daily consumed 54–56% of the microphytoplankton production. This is similar to other subtropical marine areas such as the Lagoon of Bizerte, Southwestern Mediterranean, the Eastern Equatorial Pacific and the Florida Bay (Grami et al., 2008; Richardson et al., 2003, 2004). The protozoan diet was mainly ($>70\%$) composed of microphytoplankton (Fig. 7A). Contrary to the protozoan, the metazooplankton grazed sparsely on the phytoplankton, removing only 2–12% of the microalgal production. Instead, they imposed important predatory pressure on

protozooplankton (Table 3, Fig. 7B). For example, it was mentioned that microzooplankton ingested 10 times more phytoplankton production than *Acartia tonsa*, which dominates the mesozooplankton community in Apalachicola Bay (Putland et al., 2007).

The post-bloom situation (i.e. in summer) was characterized by unusual hydrological conditions for summer season, with an absence of the thermocline and a well-mixed water column (Fig. 2). The nutrient levels were sufficient (Fig. 4), to maintain the primary production at moderate levels ($\approx 400 \text{ mg C m}^{-2} \text{ d}^{-1}$), similar to those in other areas, e.g. in the Arcachon Bay at spring time ($424 \text{ mg C m}^{-2} \text{ d}^{-1}$; Tortajada et al., 2012), in the Gulf of Biscay for the winter ($369 \text{ mg C m}^{-2} \text{ d}^{-1}$; Marquis et al., 2007) and in the northern Baltic Sea ($370 \text{ mg C m}^{-2} \text{ d}^{-1}$, Uitto et al., 1997). Large celled phytoplankton contributed almost to half of the summer primary production in both sites (Fig. 5). Nevertheless, the picophytoplankton were more productive in the Bay ($R7 = 0.26$) than in the channel ($R7 = 0.1$). This difference could be related to the differences in the composition of picophytoplankton between the sites. In these food webs, the protozooplankton consumed larger fractions of microphytoplankton production (40%) than the metazooplankton (6–9%). However, the microbivorous activity of protozoans was more intense in the Bay where small primary producers formed 52% of their diet (Fig. 7A). Consequently, the summer food web functioned as herbivorous pathway in the Channel, and as multivorous in the Bay. This seemed to be related to the change of protozoan composition, as aloricate ciliates and heterotrophic nanoflagellates (HNF) became more abundant in summer ($\approx 30\%$ of total protozooplankton) than in spring (Meddeb et al., submitted).

The situation in autumn was different between the sites (Fig. 9A, B). In the Bay, the nutrients were still available (Fig. 8 A), probably due to the vertical mixing. This promoted the production of large phytoplankton, (mic, Fig. 9A), although lower than in spring because of the decreased light and photoperiod, and the microphytoplankton remained the dominant primary producers (79%). They were also the major food source of protozooplankton (66% of their diet). Thus, the food web did not change much in structure from that in summer and continued to function as a multivorous pathway ($R7 = 0.21$). In the Channel, however, although the nutrient availability was high (Fig. 9B), the production of large algae decreased (Fig. 9B). The Channel is less deep than the Bay and therefore becomes more turbid after vertical mixing, which may have limited the production of large algae. Under these conditions, small cells are more efficient in taking advantage of the nutrients, which allowed them to form a large proportion of the primary production ($R7 = 0.6$; Fig. 9B).

Protozooplankton were mainly microbivorous, since picocells (bacteria and picophytoplankton) formed 81% of their carbon demand (Fig. 9B). Aloricate ciliates and the HNF, which were scarce during spring and summer in the Channel (0–10%), formed 50% of protozooplankton (Meddeb et al., submitted). Thus, the food web functioned approximately as a microbial pathway.

References

- Grami, B., Niquil, N., Sakka Hlaili, A., Gosselin, M., Hamel, D., Hadj Mabrouk, H., 2008. The plankton food web of the Bizerte Lagoon (South-Western Mediterranean): II. Carbon steady state modelling using inverse analysis. *Estua. Coast. Shelf.Sci.* 79, 101–113.
- Huertas, I.E., Navarro, G., Rodriguez-Gálvez, S., Lubián, L.M., 2006. Temporal patterns of carbon dioxide in relation to hydrological conditions and primary production in the northeastern shelf of the Gulf of Cadiz (SW Spain). *Deep Sea Res Part (II): Topical Studies in Oceanography.* 53, 1344–1362.
- Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A., Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the planktonic food web dynamics related to phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast. *Estuar. Coast. Shelf. Sci.* 73, 223–235.
- Meddeb, M., Grami, B., Gueroun, S.K.M., Mejri, K., Daly Yahia, M.N., Chalghaf, M., Ksouri, J., Pringault, O., Sakka Hlaili, A., (Submitted). Trophic role of microzooplankton and mesozooplankton in structuring the planktonic food web in SW Mediterranean coastal waters: a seasonal variation. *Limnol. Oceanogr.*
- Putland, J.N., R.L., Iverson., 2007. Microzooplankton: major herbivores in an estuarine planktonic food web. *Mar. Ecol. Progr. Ser.* 345, 67–73.
- Richardson, T.L., Jackson, G.A., Burd, A.B., 2003. Planktonic food web dynamics in two contrasting regions of Florida Bay. *U.S. Bulletin of Marine Science.* 73, 569–591.
- Richardson, T.L., Jackson, G.A., Ducklow, H.W., Roman, M.R., 2004. Carbon fluxes through food webs of the eastern equatorial Pacific: an inverse approach. *Deep Sea Research I.* 51, 1245–1274.
- Sakka Hlaili, A., Niquil, N., Legendre, L., 2014. Planktonic food webs revisited: Reanalysis of results from the linear inverse approach. *Prog. Oceanogr.* 120, 216–229.
- Tortajada, S., Niquil, N., Blanchet, H., Grami, B., Montanie, H., David, V., Gle, C., Saint-Beat, B., Johnson, G.A., Marquis, E., Del Amo, Y., Dubois, S., Vincent, D., Dupuy, C., Jude, F., Hartmann, H.J., Sautour, B., 2012. Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France). *Acta. Oecologica.* 40, 40–50.