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Estuarine habitats structure zooplankton communities: Implications for the pelagic trophic pathways

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ABSTRACT

Estuarine ecosystems have been described as a mosaic of habitats exhibiting different physical, biological and chemical properties and processes. These habitats are of primary importance for fishes, providing refuges and/or food for juveniles. While it is well known that habitats contribute also to the structuration of meio- and macrobenthic assemblages, this concept of habitat has never been associated to zooplankton communities, a major food resource for many pelagic fishes during summer in North-European estuaries. The objective of this work was thus to assess if estuarine habitats, in addition to the salinity gradient, structured zooplankton communities as well. Sampling was conducted at high tide during summer in a highly turbid system, the Gironde estuary, for which primary production and thus food resource at the basis of the food web is strongly limited. The results showed that even if the upstream-downstream estuarine gradient was the main factor structuring zooplankton at the scale of the estuary, there was a significant difference of zooplankton assemblages between samples collected over subtidal areas and those collected over intertidal areas. More particularly, the estuarine gradient was associated to the distribution pattern of species while difference between subtidal and intertidal samples were mainly due to difference in the level of abundance of species. Stable isotope analysis revealed that these zooplanktonic omnivorous species may be attracted to intertidal mudflats by microphytobenthos availability and that some planktivorous fishes, in particular *Alosa fallax*, preferentially fed on this zone. The role of intertidal habitats in structuring zooplankton assemblages suggests that this habitat strongly participates to the production of planktivorous species and that it represents a biotic vector of carbon resources toward subtidal areas. The loss of tidal flats habitats could thus have consequences on the functioning of pelagic system as well.

1. Introduction

Estuaries provide a variety of ecosystem services and societal benefits due to their connections with the adjoining terrestrial, freshwater and marine systems (MEA, 2005; O'Higgins et al., 2010; Barbier et al., 2011). They face rapid and strong physico-chemical fluctuations, at both spatial and temporal scales, preventing the establishment of a complex organization of the estuarine food web. This, on the other hand, is allowing the system to be both very productive and dynamically stable in terms of energy fluxes and consumer population dynamics (Moore et al., 2004; Lobry et al., 2008; Selleslagh et al., 2012a). Many marine juveniles of fishes presenting an economical interest depend on estuaries to complete their life cycle (Ray, 2005): whatever the fish feeding preference these systems provide highly nutritive environments, good environmental conditions favouring growth and, shallow turbid refuges (Beck et al., 2001; Pasquaud et al., 2010; Selleslagh et al., 2011).

Human population growth in the vicinity of estuaries has altered their structure and functioning (Elliott and Whitfield, 2011) because of excess nutrient loads (Bianchi et al., 2000), toxic pollutants (Tomlinson et al., 1980), alteration of water flows (Nilsson et al., 2005) and the loss of habitat, in particular wetlands and intertidal areas (MEA, 2005; Lotze et al., 2006). Estuarine

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ecosystems have been for a long time described as a mosaic of habitats exhibiting various physical, biological and chemical properties and processes (O'Higgins et al., 2010). These different habitats include (e.g.) subtidal or intertidal soft substratum, saltmarshes, biogenic reefs and seagrass meadows. They play a primary role as nursery for fishes and macrocrustaceans, providing refuge and/or food for juveniles (Elliott, 2002; Dahlgren et al., 2006; Holsman et al., 2006; Wouters and Cabral, 2009). Intertidal habitats, for instance display much higher primary and secondary productivity than other estuarine habitats (McLusky and Elliott, 2004). In such habitats, high organic and nutrient loads are associated with high biomasses of meio- and macrobenthic invertebrates, which in turn provide food to higher trophic levels (McLusky and Elliott, 2004). Thus, habitat structure and tidal influence contribute to the structuration of meio- and macrobenthic communities (Hosack et al., 2006; Wouters and Cabral, 2009; Blanchet et al., 2014). As a result, habitats have to be considered as subsystems within a larger ecosystem, when estimating not only the estuarine functioning but also its ecological and service values (O'Higgins et al., 2010).

This concept of habitat has never been associated to plankton communities. Ranking among the bases of aquatic food webs, plankton plays a key role in estuarine productivity, with phytoplankton turning inorganic carbon and nutrients into bioavailable organic matter and zooplankton contributing to the transfer of this primary production to higher trophic levels including commercial fishes (Lobry et al., 2008; Selleslagh et al., 2012a). In highly heterotrophic estuaries (such as the Gironde estuary), where primary production is low, zooplankton is also known to be the most important vector for carbon transfer from detritus to top predators (Tackx et al., 2003; David et al., 2006a; Lobry et al., 2008). At the estuary scale, zooplankton distribution is classically explained by the salinity gradient (Baretta and Malschaert, 1988; Mouny and Dauvin, 2002; Tackx et al., 2004; Marques et al., 2007; Modéran et al., 2010; Chaalali et al., 2013a). However, habitats (*e.g.* subtidal *versus* intertidal areas) exhibit different physical and chemical conditions associated with different types and quantity of food sources (*e.g.* phytoplankton *vs* microphytobenthos), which could in turn favour or inhibit some zooplankton species (De Jonge and Van Beusekom, 1992). In addition, the differences in benthic macrofauna assemblages between habitats (McLusky and Elliott, 2004) may imply differences in the density and assemblages of meroplankton in the above water column. As a consequence, these factors might induce further structuration of zooplankton assemblages according to habitats.

In this context, the main objective of this work was to assess if estuarine habitats, in addition to salinity gradient, participate to the structuration of zooplankton communities. This study was focused on subtidal and intertidal soft substrata, ranking among the main habitats recognized of interest for fishes (Elliott, 2002), in a highly turbid system: the Gironde Estuary (SW France). A particular attention was paid to food resources (through carbon and nitrogen stable isotopes) as a potential explaining factor of the habitat-related structuration. Implications for the trophic pathways are discussed.

2. Material and methods

2.1. Study area

The Gironde estuary is the largest SW European estuary (Fig. 1). Its surface area is about 625 km^2 at high tide and its watershed covers 81,000 km^2. Intertidal mudflats are reduced, representing approximately 8% of the estuary total area. The estuary is 76 km long between the Ocean and the Bec d'Ambès, where the Dordogne and Garonne rivers meet. This macrotidal well-mixed estuary is characterized by a large Maximum Turbidity Zone (MTZ), generated by tide asymmetry, that moves along the upstream-downstream axis according to river flow and tidal cycles (Sottolichio and Castaing, 1999). Water residence time ranges between 20 and 86 days. Particles residence time has been estimated to range in between 1 and 2 years (Jouanneau and Latouche, 1981). In the MTZ, particulate organic carbon (POC) content is very low and constant (1.5%, Etcheber et al., 2007). It is one of the most turbid estuaries in Europe with a level of suspended particulate matter (SPM) >500 mg L^{-1} (Sautour and Castel, 1995) in which primary production is strongly reduced due to light limitation. As a consequence the phytoplankton primary production has been estimated as 10 g C m^{-2} year^{-1} by Irigoien and Castel (1997). POC is mainly of terrestrial origin in the inner estuary (Savoye et al., 2012).

2.2. Sampling design and analyses

2.2.1. Zooplankton community structure

Sampling was conducted at high tide in 18 stations during July 2012 (Fig. 1). Stations were located along the salinity gradient and within two habitats: subtidal (11 stations) and intertidal (7 stations) areas. Among intertidal sampling stations, two consisted in a former artificial pond and saltmarsh system which connection with the estuary was restored 13-years ago after storm-induced collapse of the seawall. Subtidal stations were located in the 2 main channels (Médoc and Saintonge channels) and in the middle of the estuary. Intertidal stations were located along the western bank of the estuary and in the downstream Chant-Dorat flat. The former pond-saltmarsh system was located in the downstream area, in Mortagne (Fig. 1).

Prior to each zooplanktonic sampling, salinity and temperature were measured at each station with a WTW LF 197 thermo-salinometer. Sampling stations were then classified into three categories of salinity according to the Venice system (McLusky, 1993): stations where measured salinity was <5 (oligohaline conditions) were used to define the “upstream” zone of the estuary in summer (Fig. 1). Stations where salinity was comprised between 5 and 15 (mesohaline conditions) were used to define a “median” zone and stations where the salinity level was higher than 15 defined a “downstream” sector (with polyhaline conditions) (Fig. 1). The terms “polyhaline”, “mesohaline” and “oligohaline” areas were not used for these three sectors since our salinity measures were performed at high tide and corresponded to summer conditions only.

Zooplankton was collected in the top first two meters below the surface using horizontal tow using a standard 200 μm WP2 net. The volume of water filtered through the net was recorded with a Hydrobios digital flowmeter (5–10 m^3). Samples were fixed in 5% seawater/buffered formalin, sorted and identified to the lowest possible taxonomic level under a stereomicroscope. Species identification was performed on 200 individuals for “strict” zooplankton (Frontier, 1972) and on all sampled individuals for suprabenthos (i.e. mysids, amphipods, isopods, shrimps) and fish larvae. Abundances were expressed as number of individuals per m^{-3}.

Mysids, amphipods, isopods, shrimps and fishes might have avoided the 200-μm net due to their swimming abilities. A 500-μm bongo net, would indeed be more appropriate for sampling of hyperbenthic organisms in the Gironde estuary. A preliminary work however showed that a significant linear regression existed between mysid abundances estimated with a 200-μm WP2 net and a 500-μm bongo net ($n = 23$; $R^2 = 0.78$; data not shown). WP2 nets thus give a good signal of the variability of mysid densities despite a systematic underestimation of real densities. For all these