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Seasonal succession of estuarine fish, shrimps, macrozoobenthos and plankton: Physico-chemical and trophic influence. The Gironde estuary as a case study

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ABSTRACT

Characterization of the structure and seasonal variability of biotic communities is essential for a better understanding of estuarine ecosystem functioning and in order to manage these highly fluctuating and naturally stressed systems. Numerous studies have investigated the role of environmental factors in controlling temporal variations in biotic communities. However, most have concluded that the explanatory power of physico-chemical variables was significant but not sufficient to explain ecological dynamics. The present study aimed to propose the importance of trophic interactions as an additional structuring factor of species seasonal variability by examining simultaneous dynamics of all estuarine biotic communities, using the oligo-mesohaline area of the Gironde estuary (SW France) as a case study. Data on the main biological groups (fish, shrimps, macrozoobenthos and plankton) sampled during a five-year period (2004-2008) at monthly intervals using a well standardized protocol, as well as data on environmental variables, were compiled here for the first time. According to species composition, the Gironde estuary is used as a nursery, feeding, resident and migratory habitat. For almost all species, strong seasonal fluctuations occurred with a succession of species, indicating an optimization of the use of the available resources over a typical year by estuarine biological communities. Multivariate analyses discriminated four seasonal groups of species with two distinctive ecological seasons. A clear shift in July indicated a biomass transfer from a "planktonic phase" to a "bentho-demersal phase", corresponding to spring and summer-autumn periods, respectively. With regard to the temporal fluctuations of dominant species of all biological groups, this study highlighted the possible influence of trophic relationships, predation in particular, on seasonal variations in species abundance, in addition to the physico-chemical influence. This study enabled us to collate important seasonal data and to discuss their integration into seasonal models of estuarine functioning and/or specific prey-predator models. In a global change context, prey abundance variations could generate changes in the temporal dynamics of their predators (and conversely), and potentially in the functioning of the whole estuarine system.

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1. Introduction

Estuarine and coastal areas are widely considered to be among the most productive and valuable aquatic areas in the world (Day et al., 1981; Costanza et al., 1997). They are associated with important ecological functions such as primary and secondary production and nutrient cycling and provide permanent or transitory habitats for reproduction, migration, feeding and nursery for many animal species (Beck et al., 2001; Elliott and Hemingway,

2002; Gili, 2002). Due to these ecological properties, estuaries and coasts are also associated with highly valuable goods and services for human society (Costanza et al., 1997) and are consequently subjected to high human pressures such as fishing, harbour activities, dredging or industrial pumping (Post and Lundin, 1996). Estuaries are transition zones between seas and freshwater and are therefore also characterized by large fluctuations in the physicochemical conditions of the environment. As a consequence, species that inhabit such ecosystems must be able to tolerate a wide range of environmental conditions. It is now fully recognized that human activities have an increasing effect on the quality of fresh and marine waters (Vanderborght et al., 2007). In this context, the need to protect these essential habitats is becoming clear to

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authorities who have implemented directives during these last decades, such as the European Water Framework Directive or the European Marine Strategy. Implementing these directives implies, first and foremost, a better understanding of the functional aspects of ecosystem dynamics (De Jonge et al., 2006). Knowledge of the simultaneous structure and variability of the dominant biological compartments is essential for comprehending ecosystem functioning but such information is very scarce for European aquatic ecosystems, and for French estuaries in particular.

In fluctuating habitats such as temperate estuaries, biotic communities are characterized by a strong seasonal, and spatial, heterogeneity and variability (McLusky and Elliott, 2004). Such temporal variations have been attributed to fluctuations in physicochemical variables (both short- and long-term physico-chemical water conditions: e.g. wind speed and direction, turbidity, wave height, salinity, state of the tide, time of day and temperature) (Baird et al., 1991; Thiel et al., 1995; Beyst et al., 2001; McLusky and Elliott, 2004; Selleslagh and Amara, 2007, 2008a), combined with biological variables, including the timing of spawning seasons and hence the influx and efflux of individuals to and from populations (Gibson et al., 1993), food availability (Pasquaud et al., 2008), and predation pressure (Van der Veer and Bergman, 1987). However, there is still much confusion over which factor influences or controls biotic temporal variations (Beyst et al., 2001) since numerous studies dealing with this topic were based on only a limited part of the year, range of the system and specific species or assemblages. Papers dealing with the seasonal variability of fauna almost exclusively integrated physico-chemical factors, leading to poorly explained relationships ($\pm 20\%$, see Selleslagh and Amara. 2008b for example) and suggested other predictors, such as predation or competition (e.g. Marshall and Elliott, 1998). Understanding species variability requires a study at a large temporal scale and, above all, knowledge of the dynamics of other species because of interannual variations (Henderson and Bird, 2010) and biological interactions (Monaco and Ulanowicz, 1997). With increased attention to the collection of multi-year data sets, ecologists have better opportunities to test functional hypotheses driving temporal dynamics. Studying interactions between the biological compartments of an ecosystem provides a good picture of the biological community structure and is an essential step to understanding how an aquatic system functions (Thrush et al., 1999; Pasquaud et al., 2010), which is in turn essential for integrated estuarine management. It also provides a better understanding for the dynamics of ecological networks (David et al., 2006).

The Gironde estuary, in south-west France, is the largest French estuary. It is known to support a large number of fish, macrocrustacean (Lobry et al., 2006) and benthic (Bachelet, 1985) species. It is an important nursery area, a residence habitat for permanent species, as well as a migration route for amphibaline species (e.g. Rochard et al., 2001) and is also of important economic interest (G. Castelnaud, personal communication). As a consequence of many studies, the Gironde estuary is one of the most surveyed estuarine systems in France. Previous studies emphasized possible trophic implications of seasonal successions in biological assemblages (e.g. David et al., 2005, 2006; Lobry et al., 2006; Pasquaud et al., 2010). Lobry et al. (2008) first proposed an integrated picture of the whole Gironde estuarine food web using an Ecopath modelling approach at the annual level. David et al. (2006) identified predator-prey processes in the zooplankton food web and Pasquaud et al. (2010) described fish food webs at various periods of the year. However, to date no studies have combined the seasonal dynamics of all ecological compartments, particularly since macrozoobenthos sampling is recent. The aims of this study were: (1) to describe the simultaneous seasonal dynamics of fish, macrozoobenthos, shrimps and phyto- and zooplankton, considering dominant species; (2) to relate their fluctuations to environmental variables, and (3) to discuss trophic interactions structuring the seasonal dynamics of species. This work is the first analysis providing a comprehensive overview of the recent seasonal succession of biological assemblages (fish, macrozoobenthos, shrimps and plankton) in the Gironde estuary in the course of a year. The temporal changes in the main biological components of the oligomesohaline area of the Gironde were analysed to test the hypothesis that trophic interactions have the important and additional influence of physico-chemistry on the seasonal variability of estuarine communities.

2. Materials and methods

2.1. Study area

The Gironde estuary (45°20′N, 0°45′W; Fig. 1) is located in SW France and opens onto the Atlantic Ocean. This is the largest estuary in France (Lobry et al., 2003), covering an area of 625 km² at high tide. It is 12 km wide at the mouth and 76 km long to the upstream salinity limit, where the Garonne and Dordogne rivers meet. The catchment covers 81,000 km² and the mean annual rate of freshwater flow is ca.1000 m³ s $^{-1}$ (Sottolichio and Castaing, 1999). The Gironde is a macrotidal estuary with a tidal range of 4.5 m at the mouth and over 5 m at Bordeaux. The hydrodynamic conditions are highly variable due to the interaction of marine and fluvial flows,

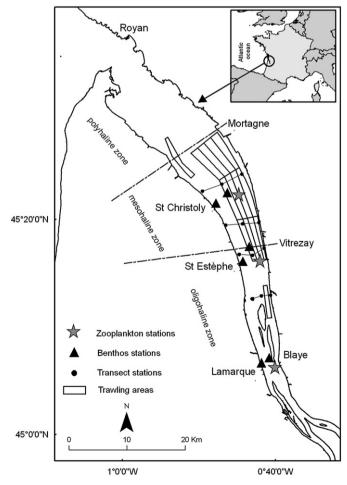


Fig. 1. Map of the Gironde estuary and location of the sampling stations and areas.

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