Journal of Sea Research 90 (2014) 95–110

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Multiscale patterns in the diversity and organization of benthic intertidal fauna among French Atlantic estuaries

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ARTICLE INFO

Article history:
Received 10 October 2013
Received in revised form 20 February 2014
Accepted 25 February 2014
Available online 6 March 2014

Keywords:
Estuaries
Macrozoobenthos
Diversity
Structuring Factors
WFD

ABSTRACT

Based on a parallel sampling conducted during autumn 2008, a comparative study of the intertidal benthic macrofauna among 10 estuarine systems located along the Channel and Atlantic coasts of France was performed in order to assess the level of fauna similarity among these sites and to identify possible environmental factors involved in the observed pattern at both large (among sites) and smaller (benthic assemblages) scales. More precisely this study focused on unraveling the observed pattern of intertidal benthic fauna composition and diversity observed at among-site scale by exploring both biotic and abiotic factors acting at the among- and within-site scales. Results showed a limited level of similarity at the among-site level in terms of intertidal benthic fauna composition and diversity. The observed pattern did not fit with existing transitional water classification methods based on fish or benthic assemblages developed in the frame of the European Water Framework Directive (WFD). More particularly, the coastal plain estuaries displayed higher among-site similarity compared to ria systems. These coastal plain estuaries were characterized by higher influence of river discharge, lower communication with the ocean and high suspended particulate matter levels. On the other hand, the ria-type systems were more dissimilar and different from the coastal plain estuaries. The level of similarity among estuaries was mainly linked to the relative extent of the intertidal "*Scrobicularia plana–Cerastoderma edule*" and "*Tellina tenuis*" or "*Venus*" communities as a possible consequence of salinity regime, suspended matter concentrations and fine particles supply with consequences on the trophic functioning, structure and organization of benthic fauna. Despite biogeographical patterns, the results also suggest that, in the context of the WFD, these estuaries should only be compared on the basis of the most common intertidal habitat occurring throughout all estuarine systems and that the EUNIS biotope classification might be used for this purpose. In addition, an original inverse relation between γ-diversity and area was shown; however, its relevance might be questioned.

1. Introduction

Elliott and Whitfield (2011) defined estuaries as "semi-enclosed coastal bodies of water which are connected to the sea either permanently or periodically, have a salinity that is different from the adjacent

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http://dx.doi.org/10.1016/j.seares.2014.02.014
1385-1101/

open ocean due to freshwater inputs, and include a characteristic biota". According to this definition, estuaries should display a characteristic benthic fauna. Benthic organisms are recognized as good indicators of environmental conditions mainly because of (1) their mostly sedentary life as adults, preventing them from escaping changing conditions, and (2) their position at the sediment–water–column interface, allowing them to integrate variations of both sub-systems (Dauvin, 1993). Most estuaries are indeed characterized by a very limited number of benthic species which number decreases as water salinity decreases (Remane, 1934; Remane and Schlieper, 1958). The scheme proposed by Remane (1934), describing the succession of marine, brackish and freshwater species along the salinity gradient in the Baltic Sea has been increasingly criticized (Attrill and Rundle, 2002; Barnes, 1989) and recently reviewed by Whitfield et al. (2012). One of the main objections to this schematic diagram is the existence of truly "brackish species" that are supposed to exclusively dwell within estuaries. Based on works conducted along the full salinity gradient within estuarine systems (e.g. Attrill and Rundle, 2002; Rodrigues et al., 2011), there is no evidence of the existence of purely brackish benthic species (Whitfield et al., 2012 and references therein). Nevertheless, a pool of typically estuarine species can be recognized. This pool of species would consist of marine euryhaline species that can live in fully marine conditions. These species however display higher occurrence, abundance and biomass levels in estuarine conditions as the abundance of more stenohaline species decreases with decreasing average level of salinity (Attrill, 2002; Little, 2000). The other main objection to the Remane's scheme is the probably most important consequences of the variability in salinity conditions than the salinity level by itself (Attrill, 2002). Nevertheless, the pattern of increasing abundance and occurrence of typically estuarine species within estuaries compared to fully marine conditions may be explained by the progressive disappearance of more competitive, but more stenohaline, species towards the head of an estuary allowing the increase of populations of typically estuarine, more euryhaline, species as they are released from interspecific competition (Little, 2000). As the salinity decreases toward the head of an estuary, typically estuarine marine species reach their tolerance limit and disappear, leading to the generally observed decrease of marine benthic species number from the downstream to the upstream areas. The particularity of these typically estuarine benthic species has lead to define them as opportunists since they only show high occurrence and abundance levels when other species disappear and they are typically retrieved in areas with very low species number. These very features of estuarine benthic fauna have lead to considerable difficulties when applying ecological quality bio-evaluation methodologies based on benthic macrofauna to estuarine systems (Blanchet et al., 2012; Elliott and Quintino, 2007). The need of appropriate methodologies to evaluate the ecological quality of European estuarine water bodies has been urged since the publication of the European Water Framework Directive (WFD). One of the main difficulties in estuarine systems is to determine appropriate reference conditions which should correspond to pristine environmental conditions. Several proposals have been made by classifying transitional water bodies into types (e.g. Barbone et al., 2012). For instance Borja et al. (2004b) used the WFD-classification to derive theoretical reference conditions for the benthos of each type of water body. More recently, Galván et al. (2010) proposed another classification of transitional water bodies with the same objective i.e. defining reference conditions for each type of estuary. The latter authors however recognized, in accordance with a growing number of studies, that benthic conditions varied greatly at finer scale within estuarine systems (Bald et al., 2005; de Paz et al., 2008; Rodrigues et al., 2011).

Given the characteristics of the typical estuarine benthic fauna and the challenges of ecological quality assessment in estuarine transitional waters, it is still necessary to evaluate the level of similarity of benthic fauna at both the among-whole estuaries scale and at the scale of similar habitat among different estuaries. In other words: are estuarine ecosystems (or estuarine ecosystem-types) comparable in terms of benthic fauna at the scale of the whole system or at least, at the scale of similar habitat among estuaries? Our study thus focused on comparing the intertidal estuarine fauna of ten estuarine systems located along the French Atlantic-Channel coast in order (1) to assess the degree of fauna similarity among estuarine systems along the French coasts and to relate observed differences to relevant physical features at the among-site scale. The results obtained will allow to evaluate the accuracy of existing typologies developed for the WFD. The second objective was (2) to relate the pattern observed at the among-site scale to finer (within-site) scale organization of benthic macrofauna and associated environmental factors. This will allow to evaluate the possibility of comparing estuarine benthic fauna among sites at a finer, biotope-scale (Ducrotoy, 2010).

2. Material and methods

2.1. Study area

The study focused on ten estuarine ecosystems located along the French coast (Fig. 1). This study included the three largest French estuaries (with surface area >190 km^2: Gironde (Gir), Loire (Loi) and Seine (Sei)) together with seven smaller estuarine systems ranging in size from 56.6 km^2 Aiguillon Sèvre Niortaise (Aig) to less than 3 km^2 (Belon (Bel) and Bidassoa (Bid)). All estuaries were influenced by tide which ranged from macrotidal to hypertidal systems (Table 1). The downstream and upstream delimitations of estuaries corresponded to the limits of water bodies defined within the European Water Framework Directive (WFD).

2.2. Physical descriptors

The total area of each estuary was retrieved from the WFD-map using ARCGIS 9. Intertidal areas were obtained from the literature including Nicolas et al. (2010). In order to assess resemblance among the ten sites and to relate observed patterns to general hydrological,

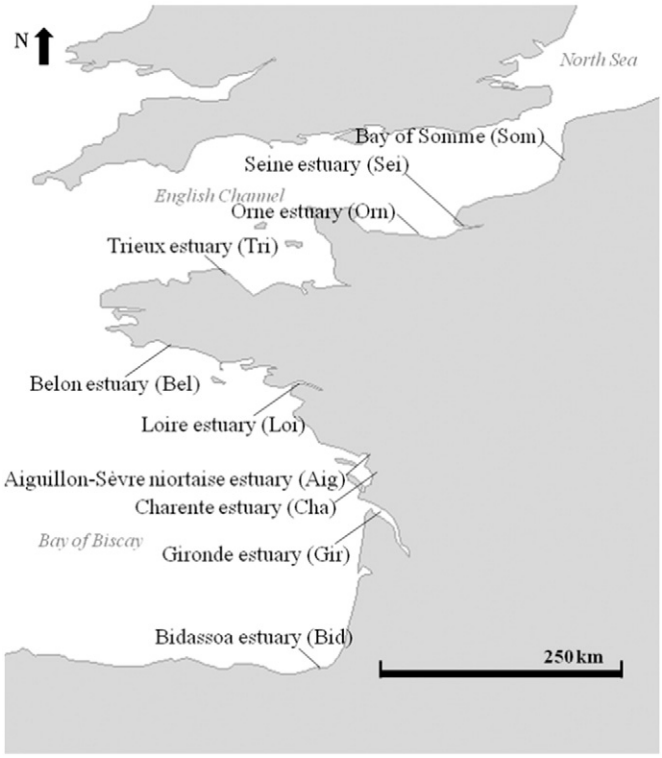

Fig. 1. Location of the ten study sites along the French coast.