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Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France

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ABSTRACT

When the Pacific oyster (*Crassostrea gigas*, Thunberg) was introduced into France for aquaculture in the mid-sixties, it was initially confined to the sites where it was farmed. Subsequent global warming most likely facilitated the establishment of wild populations throughout the French coastline. This phenomenon of spread has become so great that oyster reefs have recently appeared in sheltered estuaries, on both soft and hard substrate. The present study examined two such sites in the Bay of Brest, Brittany. It is the first to investigate the impacts of this new substrate on the biocoenosis of uncolonised intertidal habitats in France. Increased species richness and abundance of intertidal macrofauna were observed in the presence of oyster reefs on both, mud (4 and 20 fold respectively) and rock (5 fold for both). The dominance of suspension feeders in mud changed to carnivores in reefs and their underlying sediment. Calculation of biotic coefficients (BC) of the soft-bottom fauna revealed only a slight organic enrichment, and the organic and silt composition in the sediment beneath oyster reefs were not significantly different from that on bare sites. On rock, the dominance of grazers remained unchanged between bare rock and oyster reef, while reef on rock was also characterised by deposit and detritic feeders. *C. gigas* is suspected to cause a homogenisation of coastal habitats with an impoverishment of overall quality but we detected only 11 common species between reefs on mud (60 species) and those on rock (55 species).

1. Introduction

Introduced marine species are known to have an impact on native ecosystems, especially on very productive systems like those in coastal regions and estuaries, which have high biodiversity (Ruiz et al., 1997; Cohen and Carlton, 1998; Ruiz et al., 1999; Wasson et al., 2005). Although only a few introduced species (10–15%) are considered as pests (Williamson and Fitter, 1996; Ruiz et al., 1997), most studies show undesirable effects of invasive species on native biodiversity, community structure and function, genetic diversity, population dynamics, economy, and even human health (Ruiz et al., 1997; Parker et al., 1999; Mack et al., 2000; Grosholz, 2002).

However, although it cannot be denied that introduced species are capable of causing dramatic damaging effects on the ecosystems they invade, some studies show that such invaders are not always as bad as they might seem (Thieltges et al., 2006). This ambivalence is illustrated by the example of the American slipper limpet *Crepidula fornicata* (Thieltges et al., 2006), which was accidentally introduced into Europe from the Eastern coast of America at the end of the nineteenth century and now extends along European coasts from Spain to Norway (Blanchard, 1997). In localised areas, such as some of the places it has colonised in France, populations reach very high densities (1000 individuals m^{-2}) that can have detrimental ecological impacts like: increased siltation related to pseudofaeces and faeces production (Erhold et al., 1998), lowering of native species recruitment by spatial competition processes (Thouzeau et al., 2000), and alteration of benthic community structure (Thouzeau et al., 2000; Chauvaud et al., 2003a,b). However, in certain situations, this invasion has had positive effects. One study showed that *C. fornicata* protects the Bay of Brest (France) from toxic algal blooms by changing plankton composition and food web structure (Chauvaud et al., 2000). The extensive spread of *C. fornicata* has increased suspension feeder biomass and therefore increased biodeposition, which has then enhanced biogenic silica retention in the bay. Recycling of biogenic silica through the summer maintains diatom populations and limits chronic toxic algal blooms occurring in eutrophic conditions (Chauvaud et al., 2000; Ragueneau et al., 2002, 2005).

In the present study we examined ecological impacts of another non-indigenous species, the Pacific oyster *Crassostrea gigas*, on intertidal communities of the coastal ecosystem of the Bay of Brest (France). Pacific oysters have been intentionally introduced into 66 countries for aquaculture (Ruesink et al., 2005) and self-sustaining

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populations have today become established in 17 of these. In some of these countries *C.gigas* has been revealed to be more competitive than native oyster species, such as in New Zealand where *C.gigas* rapidly out-recruited the native *Saccostrea comercialis* (Dinamani, 1991). The same type of competition was observed in Australia where,30 years after its introduction *C.gigas* recruitment dominated that of *S. commercialis* (Chew, 1990). Reise (1998), Diederich (2005, 2006) and Schmidt et al. (2008) showed that the native intertidal blue mussel beds in the Wadden Sea had become overgrown by Pacific oysters but had not been replaced by them (Fey et al., 2010). Markert et al. (2010) found that Pacific oyster reefs were higher in diversity than native blue mussel beds, promoting epibenthic species of the Wadden Sea. In Willapa Bay, the comparison of native intertidal mudflat and oyster-dominated habitats as well showed that oysters harboured a higher diversity of epifauna (Hosack et al., 2006). Ecological effects of invasive Pacific oysters on intertidal communities have been very little examined so far, especially on rocky communities for which only one study is known (Escapa et al., 2004).

C. gigas was intentionally introduced into France at the end of the 1960 s to replace cultivated oyster stocks of *Ostrea edulis* and *Crassostrea angulata* decimated by disease (Grizel and Heral, 1991). For more than 20 years *C. gigas* did not reproduce in Brittany. Because *C. gigas* is a subtropical species, its minimal temperature requirement for spawning is above 18 °C (Mann, 1979) and the water was simply not warm enough on this part of the French coast. However, with the rise in temperature that has occurred over recent decades, environmental conditions in Brittany became favourable for spawning and *C. gigas* started to reproduce there in the 1990s (Lejart, 2009). Today, wild sustainable populations have become established in the intertidal zone all along the Brittany coast. Although populations are found on exposed oceanic shores, the highest densities, with more than 1000 individuals m^{-2} (Lejart and Hily, 2005), are reached in estuarine and sheltered habitats. Over the last few years, particularly on soft sediment but more recently even on rocks, oysters have become so abundant that one can observe the formation of oyster reefs. That is particularly the case in the Bay of Brest where the total stock of wild oysters was estimated at 10 000 tons in 2005 (Lejart and Hily, 2005). Although the presence of oysters on the Brittany shore is now common, oyster reefs are new biogenic structures on these coasts. We are therefore witnessing a drastic change in the intertidal landscape. In the United States, oyster reefs of *Crassostrea virginica*, are seen as a valuable habitat that needs to be restored and protected from overfishing (Coen and Luckenbach, 2000; Peterson et al., 2003; Rodney and Paynter, 2006). The situation is however very different in France as the new oyster reefs are not native, but the result of the settlement and spread of an alien species. The present study is the first to investigate the influences of this species on intertidal communities in France. Its goal was to examine the oyster reefs formed by invasive *C. gigas* in Brittany by addressing three basic questions: 1) Can we consider these reefs as a new biogenic habitat? 2) Can we detect differential responses of benthic macrofaunal organisms to the formation of oyster reefs on mud and on rock? 3) Does this new habitat induce a homogenization of intertidal communities?

2. Materials and methods

2.1. Study area

The study was carried out in the Bay of Brest, western Brittany (France), in January 2006. This shallow semi-enclosed coastal bay covers 180 km^2 and is connected to the Atlantic Ocean by a small strait (1.8 km wide, 50 m deep). Freshwater entering the bay is mostly (80%) brought in by two rivers, the Elorn in the North of the bay and the Aulne in the South.

The Bay of Brest is a shallow (mean depth 8 m) macrotidal coastal system. Less than 50% of the bay is deeper than 5 m and, as the tide can rise and fall by as much as 8 m, a very large intertidal surface of substrate is available for potential colonisation by oysters. Oysters were introduced into the Bay of Brest at the beginning of the seventies but the invasion did not start until the nineties and massive spread has only been observed since 2000. In 2005, this colonised surface was estimated at 3 km^2 with a mean oyster density of 84 individuals m^{-2} (Lejart and Hily, 2005). Hard and soft sustrate are both colonised. As oyster larvae need a support to settle, pebbles and shells existing on mudflat were used by the first individuals to arrive. This phenomenon has been also seen by Troost (2010). Then, as *C.gigas* settles preferentially on conspecifics rather than on any other substrate (Diederich, 2005), reefs developed progressively.

Sampling was done in January 2006. Two sampling sites were chosen in sheltered areas in the South-East of the bay, near the Aulne estuary (Fig. 1), where oyster reefs had formed on natural

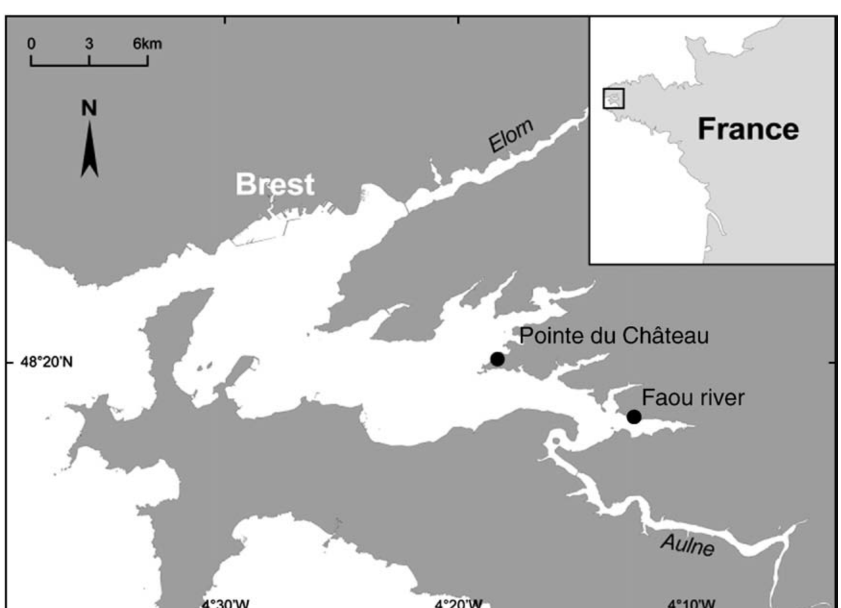

Fig. 1. Study area in the west of Brittany (France) and location of experimental sites: Pointe du Château and Faou river.