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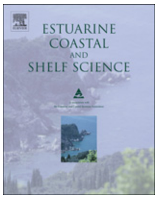

Variations in the pallial organ sizes of the invasive oyster, *Crassostrea gigas*, along an extreme turbidity gradient

Mickaël Dutertre [a,*], Laurent Barillé [a], Peter G. Beninger [a], Philippe Rosa [a], Yves Gruet [b]

[a] *Université de Nantes, Nantes Atlantique Universités, EA 2160 Mer-Molécules-Santé, Faculté des Sciences et des Techniques, BP 92208, 2 rue de la Houssinière, Nantes F-44322, France*

[b] *Bio-littoral, Université de Nantes, Faculté des Sciences et des Techniques, BP 92208, 2 rue de la Houssinière, Nantes F-44322, France*

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ABSTRACT

Spatial size variations of labial palps, gills and the adductor muscle of the invasive feral oyster, *Crassostrea gigas*, were studied along two gradients of suspended particulate matter (SPM) concentrations in the temperate macrotidal Bourgneuf Bay, (annual mean SPM concentration gradient of 21.0–154.0 mg l^{-1}) and the adjacent Loire Estuary (annual mean SPM concentration gradient of 24.1–630.4 mg l^{-1}) on the French Atlantic Coast. The gill-to-palp (G:P) ratios decreased with increasing turbidity, both in the bay and the estuary. Changes in G:P ratios were chiefly related to palp area variations, increasing gradually from low turbidity to very high-turbidity sites, while gill area showed no clear relationship with turbidity conditions. The G:P ratio, showing a significant relationship ($r^2 = 0.97$) with SPM concentrations, is proposed as a pallial organ index of oyster acclimation to turbidity conditions. The area of the striated part of the adductor muscle was always greater than that of the smooth one, and adductor muscle area tended to decrease when SPM concentration increased. These observations show the morphological capacity of the oyster *C. gigas* to tolerate SPM concentrations above the feeding cessation thresholds previously determined experimentally. They also suggest that pallial organ size variations could help explain the success of recent feral oyster invasions in temperate turbid ecosystems.

1. Introduction

The Pacific cupped oyster, *Crassostrea gigas*, was deliberately introduced to worldwide coastal waters for aquaculture in the twentieth century. In northern European temperate ecosystems, *C. gigas* has become an invasive species due to the recent extension and proliferation of feral populations (Reise et al., 1999; Wehrmann et al., 2000; Cognie et al., 2006). It is assumed that the proliferation of *C. gigas* in European farming areas is attributed to a rise in water temperature over the past decades, allowing successful reproduction, larval development, and settlement (Diederich et al., 2005; Dutertre et al., in press a,b). However, high densities of feral *C. gigas* are found not only in the oyster-farming areas but also outside them, notably in high-turbidity estuaries. This is even more remarkable since, the few available data concerning the turbidity of their native range in Japan indicate that *C. gigas* is farmed in low turbidity conditions (Ventilla, 1984; Fujisawa et al., 1987; Kobayashi et al., 1997). To date, functional SPM thresholds have been determined in laboratory experiments and subsequently used in current models; these suggest a cessation of filtration and selection activities at 192 mg l^{-1} and 150 mg l^{-1}, respectively, which correspond to SPM concentrations markedly lower than those encountered by some feral *C. gigas* populations, which nevertheless seem to thrive in very high-turbidity ecosystems (Deslous-Paoli et al., 1992; Pastoureaud et al., 1996; Barillé et al., 1997b). Considering the role of this reef-building oyster as an ecosystem engineer and its economic interest (see Ruesink et al., 2005 for a review), it would be interesting to determine the underlying mechanisms enabling *C. gigas* to invade very high-turbidity coastal ecosystems.

In suspension-feeding bivalves, pre-ingestive particle processing is performed by gills and/or labial palps (Newell and Jordan, 1983; Ward et al., 1991; Beninger et al., 1992, 2004; Beninger and St-Jean, 1997; Cognie et al., 2003; Ward and Shumway, 2004). Intraspecific pallial organ variations, characterized by smaller gills and larger palps when seston concentration increases, have mainly been described in bivalves with a functionally homorhabdic (*sensu* Beninger and Decottignies, 2008) gill structure (Theisen, 1982; Essink et al., 1989; Payne et al., 1995a,b; Drent et al., 2004), in which post-capture particle selection occurs only on the palps (Beninger et al., 1997; Beninger and St-Jean, 1997; Ward et al., 1998). However, recent

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[*] Corresponding author. Tel.: +33 2 51 12 56 91; fax: +33 2 51 12 56 68.
E-mail address: mickael.dutertre@univ-nantes.fr (M. Dutertre).

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studies on the functionally heterorhabdic pseudolamellibranch *Crassostrea gigas* have shown a relationship between gill and palp sizes, and particle clearance and selection efficiency, at different turbidity levels (Dutertre et al., 2007). These studies suggest that *C. gigas* gill size variations could be more complex than the generally-observed morphological trend (Barillé et al., 2000; Honkoop et al., 2003; Dutertre et al., 2007; Dutertre, 2008), potentially in relation to the particularly complex functionally heterorhabdic gill structure, which enables particle selection and ingestion volume regulation to be carried out on both gills and palps (Cognie et al., 2003; Beninger et al., 2005, 2008).

In high-turbidity ecosystems where *Crassostrea gigas* is now invasive, delimiting the range of SPM concentrations it can tolerate is of prime importance, especially for integration into predictive ecophysiological models of growth performance and population dynamics (Barillé et al., 1997a; Kobayashi et al., 1997; van der Meer, 2006). It is thus interesting to determine whether the observed phenotypic plasticity of the *C. gigas* pallial organs may be a factor in the extension of this species' range of tolerated turbidity conditions. An intraspecific relationship between pallial organ size and SPM concentrations should therefore be quantified not only to answer this question, but also to adapt feeding thresholds integrated into ecophysiological models, and for use as a time-integrated indicator of turbidity conditions (Payne et al., 1995b).

Previous studies suggest that, although not directly involved in particle processing, the oyster adductor muscle size may also be an indicator of turbidity conditions (Yonge, 1936; Barillé et al., 2000). Bivalve adductor muscle consists of a smooth part, responsible for prolonged valve closure in unfavorable external conditions, and a striated part, mediating rapid closure of valves in response to predator attack or waste ejection from the pallial cavity (Yonge, 1936; Morrison, 1996). Just as adductor muscle size has been observed to vary in mussels in relation to predation pressure (Hancock, 1965; Theisen, 1982), so it may be hypothesized that frequent and strong valve claps, resulting from the accumulation of large amounts of rejected particles in the pallial cavity under high-turbidity conditions, might produce an increase in the size of the striated adductor muscle.

The aim of the present work was to investigate the potential relationship between extreme SPM gradient and the size variations of feral *Crassostrea gigas* palps, gills and adductor muscle, in Bourgneuf Bay, an important French oyster-farming area, and the adjacent Loire Estuary. A further objective was to establish a quantitative relationship between *C. gigas* G:P ratios and SPM concentrations.

2. Materials and methods

2.1. Environmental characteristics

Bourgneuf Bay and the Loire Estuary are northern temperate ecosystems subject to a combination of seasonal and short-term variations in hydrological parameters. Bourgneuf Bay, a macrotidal shellfish ecosystem on the French Atlantic Coast, is characterized by a marked turbidity gradient, decreasing from North (annual mean SPM concentration = 154.0 mg l^{-1}) to South (annual mean SPM concentration = 33.8 mg l^{-1}) and from East to West (annual mean SPM concentration = 21.0 mg l^{-1}) (Table 1; Haure and Baud, 1995; IFREMER, Quadrige Database 2004). The northern high turbidity (HT) site of La Coupelasse is an oyster-farming area located on a mudflat while the southern intermediate turbidity (IT) site, Gresseloup, is a sandy-muddy farming area. At the entrance of the bay, the western low turbidity (LT) sites, Cobe's Rock and Cape Herbaudière, are characterized by sandy sediment and rocky areas. The mean annual salinity in Bourgneuf Bay is 32.5–33.9 psu.

Table 1
Characteristics of the sampling sites of feral oysters, *Crassostrea gigas*, in Bourgneuf Bay (first four sites) and the adjacent Loire Estuary (last four sites). SPM: suspended particulate matter. HT: high turbidity; IT: intermediate turbidity; LT: low turbidity; VHT: very high turbidity

Sampling site	Co-ordinates	Annual mean SPM (mg l^{-1})	Turbidity condition
Cape Herbaudière	47° 1′ 39.9″ N 2° 18′ 32.1″ W	21.0[a]	LT
Cobe's Rock	47° 1′ 10.0″ N 2° 13′ 35.3″ W	24.3[b]	LT
Gresseloup	46° 57′ 2.6″ N 2° 7′ 53.4″ W	33.8[c]	IT
La Coupelasse	47° 1′ 34.7″ N 2° 1′ 55.9″ W	154.0[c]	HT
Cape Saint-Gildas	47° 7′ 58.3″ N 2° 15′ 2.3″ W	24.1[b]	LT
Tharon-Plage	47° 10′ 40.7″ N 2° 9′ 54.9″ W	dpa[d]	IT
Mindin	47° 16′ 3.4″ N 2° 10′ 16.8″ W	dpa[d]	VHT
Paimboeuf	47° 17′ 25.8″ N 2° 1′ 57.5″ W	630.4[e]	VHT

[a] Decottignies P., Université de Nantes, unpublished data.
[b] IFREMER, Quadrige Database 2004.
[c] Haure and Baud, 1995.
[d] Froidefond et al., 2003 (data partially available).
[e] GIP Loire Estuaire, MECEL Database 2007.

The Loire Estuary has a mean annual flow of 853 $m^3 s^{-1}$, with peak floods in winter reaching 4000 $m^3 s^{-1}$, while summer flows can be as low as 100 $m^3 s^{-1}$. SPM concentrations vary from 10 to more than 2000 mg l^{-1} in the maximum turbidity area (Froidefond et al., 2003). The Loire estuary shows a decreasing SPM gradient seaward. The four selected stations (Table 1, Fig. 1) encompass two

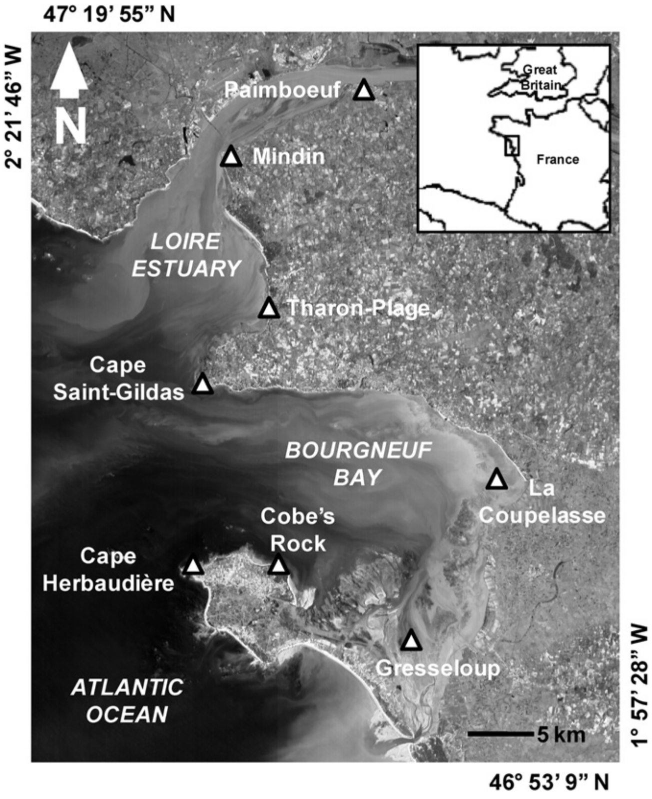

Fig. 1. Map of France showing location of study area and sampling sites (**Δ**) of oysters, *Crassostrea gigas*, in Bourgneuf Bay and the Loire Estuary (SPOT satellite image).