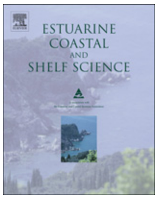
Estuarine, Coastal and Shelf Science 85 (2009) 431–436

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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



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

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ARTICLE INFO

Article history:
Received 25 May 2009
Accepted 7 September 2009
Available online 11 September 2009

Keywords:
adductor muscle
Crassostrea gigas
gills
invasive oyster
palps
turbidity
France
Bourgneuf Bay
Loire Estuary

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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doi:10.1016/j.ecss.2009.09.007

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

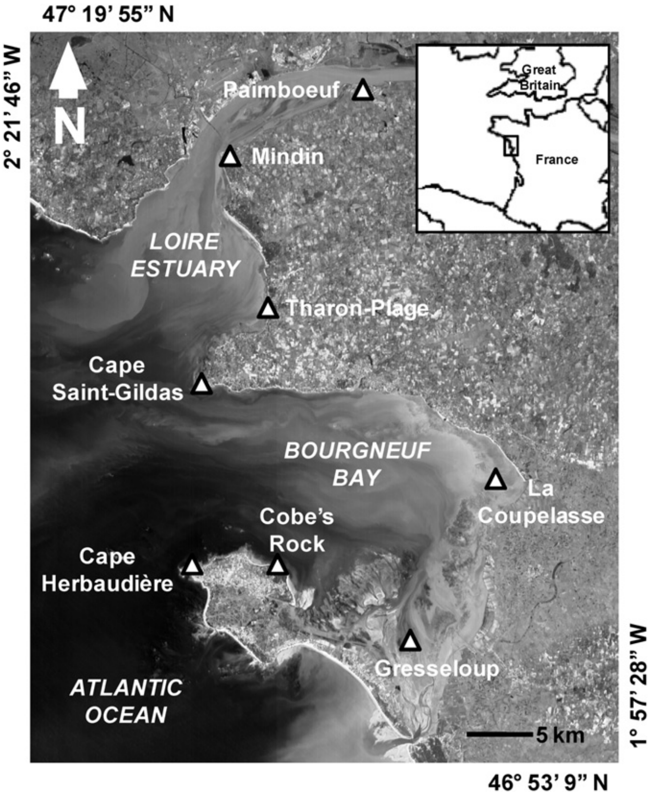

Fig. 1. Map of France showing location of study area and sampling sites (**Δ**) of oysters, *Crassostrea gigas*, in Bourgneuf Bay and the Loire Estuary (SPOT satellite image).

stations at the outer estuary, Cape Saint-Gildas (low turbidity, LT) and Tharon-Plage (IT), and two others at Mindin (very high turbidity, VHT) and Paimboeuf (VHT) in the polyhaline sector (30–16 psu) of the inner estuary. Mean annual SPM concentrations were obtained from different monitoring programs (IFREMER, Quadrige Database 2004; GIP Loire Estuaire, MECEL Database 2007). For two stations (Tharon-Plage and Mindin), only partial turbidity data were available (irregular satellite readings – Froidefond et al., 2003), so these stations were not used for determination of the pallial organ index.

2.2. Feral oyster sampling and maintenance

Feral oysters were collected at eight sites in Bourgneuf Bay (November 2004) and the adjacent Loire Estuary (December 2007), along the French Atlantic Coast (Fig. 1, Table 1). Adult feral oysters were selected, on rocky substrates, within a shell length range of 7–10 cm in order to reduce the variability linked to animal size. Nevertheless, natural growth conditions lead to a high variability in oyster shell shape, especially when a crowding effect, related to the scarcity of rocky substrates, is associated with the longitudinal growth of the shell (Orton, 1936; Gunter, 1938; Galtsoff, 1964). A possible effect of shell shape, described by length-to-width (L:W), on gill-to-palp ratios was tested; subsequent comparisons between oysters required a standardization of the pallial organ measurements to those of an equivalent individual of 1 g dry tissue mass in order to take into account the influence of different sizes and ages (Andrews, 1979).

Since glycogen cells are a major component of oyster palps (Berthelin et al., 2000), we performed these measurements at the end of the reproductive season, to avoid palp size changes due to glycogen storage or utilization. The same day of their sampling, individuals were taken to the laboratory and manually cleaned of their shell epibionts, prior to biometric and pallial organ measurements.

2.3. Biometric measurements

Measurements were performed on thirty oysters sampled in each of the eight sites in Bourgneuf Bay and the Loire Estuary. Shell dimensions (mm) were measured with a caliper to obtain length, width, length-to-width (L:W) ratio and height. The right valve was removed to take digital photographs of the pallial organs, on which areas were delineated and calculated with LUCIA G 4.80 image analysis software (Image Analysis Systems). The functional association of gills and palps in oysters can be expressed as the gill-to-palp (G:P) ratio. Gill and palp sizes were estimated from the areas of the outer right gill lamella and labial palp, and G:P was calculated. The striated, smooth, and total adductor muscle areas were estimated from their transverse sections, and all soft parts were then dried at 60 °C for 48 h to obtain the dry tissue mass (DTM, g). As shell dimension and soft tissue mass are not influenced in the same way by environmental variations (Hilbish, 1986), morphological responses involving pallial organs of bivalves are commonly standardized to those of an equivalent individual of 1 g DTM as follows (Bayne et al., 1987; Barillé et al., 2000):

$$\mathrm{POA_s} = (1/\mathrm{DTM})^{b} \times \mathrm{POA_{ex}}$$

where $\mathrm{POA_s}$ represents the pallial organ area for the standard oyster, $\mathrm{POA_{ex}}$ is the experimental value and b the allometric exponents determined by Barillé et al. (2000).

2.4. Statistical analysis

Sigmastat 3.1 (Systat software) was used for all statistical analyses. After checking the normality and heteroscedasticity of the distributions, one-way or two-way parametric ANOVA was performed. Where appropriate, Student–Newman–Keuls (SNK) tests were then carried out *a posteriori*. Non-parametric Spearman tests were also used to determine correlations between distributions (Conover, 1999). Variations in G:P ratio were fitted against log(SPM concentrations) using an inverse polynomial model $y = a + (b/x) + (c/x^2)$ which was tested by analysis of variance.

3. Results

Differences in oyster shell shape (Table 2, one-way ANOVA, $df = 7$, $F = 47.59$, $p < 0.01$) were considered with regard to the length:width ratio (L:W). Shells showed a similar sub-circular shape (L:W = 1.4–1.7) in most of the sampling sites, but they were longer and thinner (L:W = 2.3–2.6) in the oyster-farming sites of La Coupelasse and Gresseloup (SNK-tests, $p < 0.01$), characterized by a sparseness of rocks for attachment. However, L:W ratios were not correlated to G:P ratios (Spearman correlation test, $n = 8$, $r = -0.59$, $p = 0.34$) indicating that shell shape did not significantly influence the size of the pallial organs.

Significant variations were recorded for gill areas between the different turbidity sites of Bourgneuf Bay and the Loire Estuary (Fig. 2A, one-way ANOVA, $df = 7$, $F = 9.70$, $p < 0.01$), palp areas (Fig. 2B, one-way ANOVA, $df = 7$, $F = 82.17$, $p < 0.01$) and G:P ratios (Fig. 2C, one-way ANOVA, $df = 7$, $F = 36.62$, $p < 0.01$). Gill area was significantly larger at the VHT site and smaller at the LT site without any trend related to turbidity (Fig. 2A, SNK-tests, $p < 0.01$ and $p < 0.05$, respectively). In contrast, a positive relationship between palp area and turbidity was observed both in the bay and in the estuary (Fig. 2B). Palps were significantly smaller at the LT sites (SNK-test, $p < 0.01$), while they were significantly larger at the VHT sites (SNK-test, $p < 0.01$).

Although there was no correlation between gill and palp area variations (Spearman test, $n = 8$, $r = 0.30$, $p = 0.41$), two clear gradients were established with the G:P ratios, showing significantly higher values at the LT sites (Fig. 2C, SNK-test, $p < 0.01$) and significantly lower values at the VHT sites (SNK-test, $p < 0.01$). G:P ratios were negatively correlated with palp areas (Spearman correlation test, $n = 8$, $r = -0.93$, $p < 0.01$), while no correlation was found with

Table 2
Mean (±SD) shell measurements (length, width, length:width (L:W) ratio and height) and proportion of the striated part of the adductor muscle in feral oysters, *Crassostrea gigas*, collected from different turbid sites of Bourgneuf Bay (first four sites) and the adjacent Loire Estuary (last four sites)

Sampling site	*n*	Shell length (mm)	Shell width (mm)	L:W ratio	Shell height (mm)	Striated area (%)
Cape Herbaudière	30	70.3 ± 9.5	50.1 ± 9.2	1.4 ± 0.3	21.4 ± 4.1	57.2 ± 6.2
Cobe's Rock	30	84.5 ± 11.0	51.3 ± 8.3	1.7 ± 0.3	23.2 ± 4.1	55.0 ± 7.9
Gresseloup	30	103.3 ± 12.1	46.2 ± 5.0	2.3 ± 0.3	25.4 ± 4.1	53.7 ± 6.6
La Coupelasse	30	104.0 ± 11.3	40.7 ± 5.3	2.6 ± 0.4	25.9 ± 2.8	56.1 ± 5.5
Cape Saint-Gildas	30	83.0 ± 8.3	57.6 ± 5.8	1.5 ± 0.2	18.1 ± 3.1	56.9 ± 7.6
Tharon-Plage	30	76.8 ± 9.3	51.3 ± 7.8	1.5 ± 0.2	30.3 ± 9.5	60.9 ± 4.8
Mindin	30	85.1 ± 11.2	54.5 ± 10.5	1.6 ± 0.3	29.8 ± 7.5	65.8 ± 4.4
Paimboeuf	30	80.1 ± 10.4	50.0 ± 8.2	1.6 ± 0.3	21.4 ± 5.0	64.0 ± 6.0

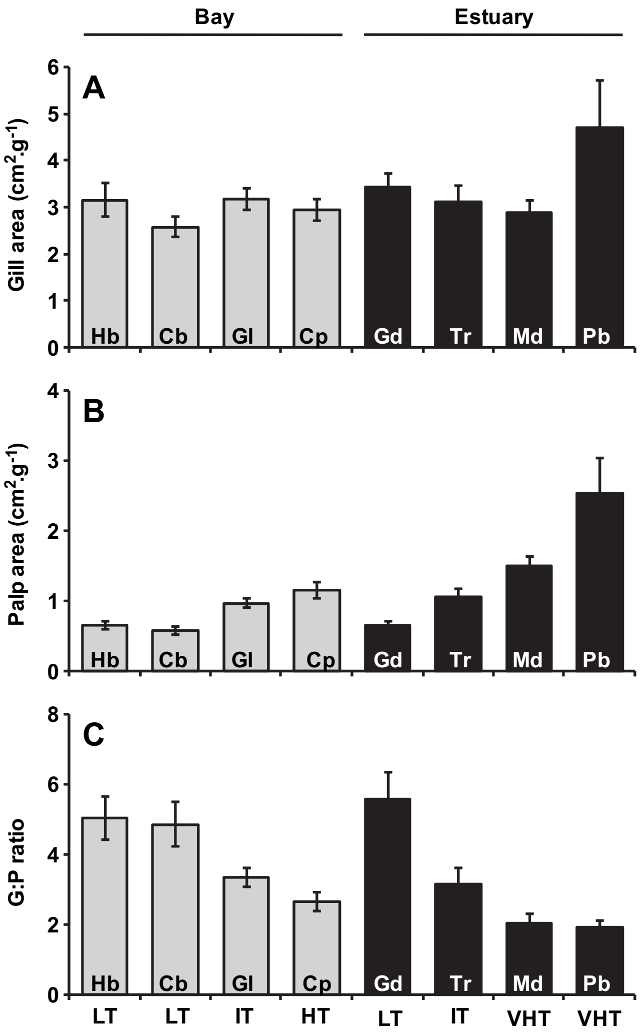

Fig. 2. Mean areas (±95% CI; $n = 30$) of palps (A), gills (B) and gill-to-palp (G:P) ratio (C) standardized to a feral oyster of 1 g dry tissue mass, from different turbid sites in Bourgneuf Bay and the Loire Estuary. Cb: Cobe's Rock; Cp: Coupelasse; Gd: Cape Saint-Gildas; Gl: Gresseloup; Hb: Cape Herbaudière; HT: high turbidity; IT: intermediate turbidity; LT: low turbidity; Md: Mindin; Pb: Paimboeuf; Tr: Tharon-Plage; VHT: very high turbidity.

gill areas (Spearman correlation test, $n = 8$, $r = -0.07$, $p = 0.84$). A significant quantitative relationship was established between G:P ratios and annual mean SPM concentrations (Fig. 3, one-way ANOVA, $p < 0.05$, $\log(\mathrm{SPM}) = 1.08 + (0.19/(\mathrm{G{:}P\ ratio})) + (6.21/(\mathrm{G{:}P\ ratio})^2)$, $n = 6$, $r^2 = 0.97$).

The adductor muscle area of feral oysters showed significant variations according to the differing turbidity sites of Bourgneuf Bay and the Loire Estuary (Fig. 4, one-way ANOVA, $df = 7$, $F = 18.31$, $p < 0.01$). Adductor muscle area was significantly largest at the LT sites (SNK-test, $p < 0.05$), while it was smallest in the VHT conditions of Mindin (SNK-test, $p < 0.01$). The proportion of the striated area of the adductor muscle was always higher than the smooth area at each site (Table 2, two-way ANOVA, $df = 1$, $F = 122.42$, $p < 0.01$).

4. Discussion

4.1. Relationship between SPM concentration and pallial organ areas

G:P varied inversely with turbidity (21.0–154 mg l^{-1} in the macrotidal bay; 24.1–630.4 mg l^{-1} in the estuary), suggesting a role

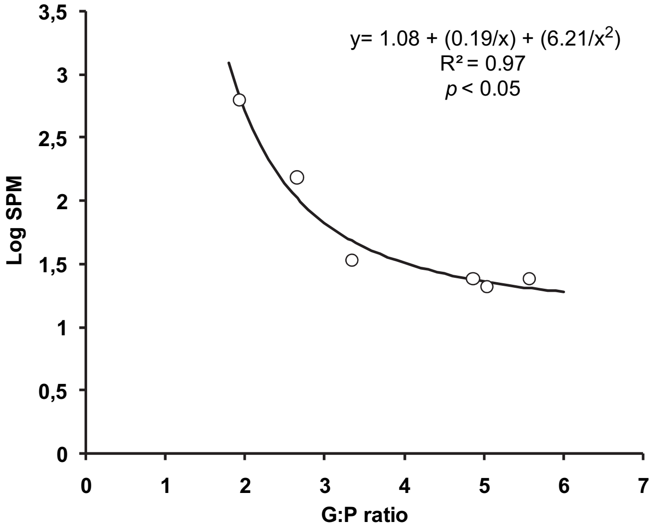

Fig. 3. Relationship ($\log(\mathrm{SPM}) = 1.08 + (0.19/(\mathrm{G{:}P\ ratio})) + (6.21/(\mathrm{G{:}P\ ratio})^2)$, $n = 6$, $r^2 = 0.97$) between gill-to-palp (G:P) ratios and suspended particulate matter (SPM) concentrations for feral oysters, *Crassostrea gigas*, living in different turbidity conditions in Bourgneuf Bay and the Loire Estuary on the French Atlantic Coast.

of the relative pallial organ sizes in the tolerance of feral oysters to turbid conditions. However, taken separately, pallial organ variations showed some differences with the intraspecific trend observed in functionally homorhabdic bivalves (Theisen, 1982; Essink et al., 1989; Payne et al., 1995a; Barillé et al., 2000; Dutertre et al., 2007). Indeed, while the *Crassostrea gigas* palp area clearly showed significant enlargement with increasing turbidity, gill area variations were less marked, despite a general decreasing trend in the bay (between IT and HT sites) and the adjacent estuary (between LT and VHT sites). As it is recognized that feeding rates of suspension-feeding bivalves are related to feeding organ size (Kiørboe and Møhlenberg, 1981; Jones et al., 1992; Franz, 1993; Pouvreau et al., 1999; Dutertre et al., 2007), smaller gills in high-turbidity conditions have been hypothesized to reduce the amount of cleared particles to be processed by palps. In functionally homorhabdic bivalves, this mechanism probably avoids overloading the palps, which are the only pallial organ involved in post-capture particle selection and ingestion volume regulation (Beninger and St-Jean, 1997; Ward et al., 1998). However, the capacity of oysters to qualitatively select particles first on their heterorhabdic gills, allows

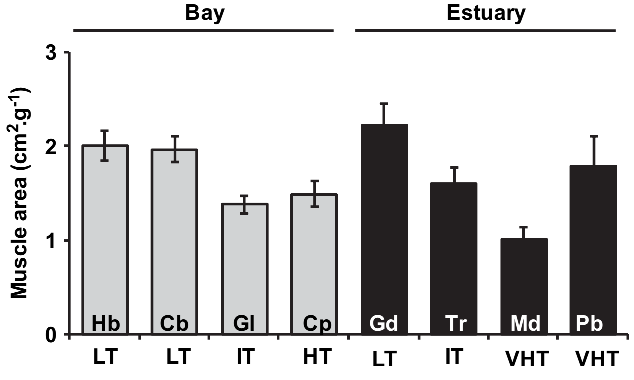

Fig. 4. Mean areas (±95% CI; $n = 30$) of the adductor muscle standardized to a feral oyster of 1 g dry tissue mass, from the different turbid sites in Bourgneuf Bay and the Loire Estuary. Cb: Cobe's Rock; Cp: Coupelasse; Gd: Cape Saint-Gildas; Gl: Gresseloup; Hb: Cape Herbaudière; HT: high turbidity; IT: intermediate turbidity; LT: low turbidity; Md: Mindin; Pb: Paimboeuf; Tr: Tharon-Plage; VHT: very high turbidity.

a reduction in the amount of particles transferred to the palps without a reduction in the clearance rate and/or gill area (Cognie et al., 2003; Beninger et al., 2008). Indeed, small gills have been linked with increases in clearance rate and particle selection efficiency, enhanced by large palps, in *C. gigas* exposed to high SPM concentrations (Dutertre et al., 2007). Furthermore, it should be noted that in oysters, the inverse relationship between the annual mean SPM concentrations and the G:P ratios is chiefly the result of the palp area variations. However, although gill and palp sizes generally varied in opposite ways, at the most upstream site of the Loire Estuary, the lower salinity might have caused an increase in pallial organ cell volume (Neufeld and Wright, 1996), and, consequently, an overestimation of the gill and palp sizes.

Contrary to expectations, adductor muscle area tended to decrease when SPM concentration increased. In most oceanic LT sites, larger adductor muscle area could be associated with predator pressure due to the abundance of the starfish *Asterias rubens*, as previously observed in mussels (Hancock, 1965; Theisen, 1982). A larger striated part of the adductor muscle, which allows a more efficient ejection of waste particulate material from the pallial cavity, was attributed to the ability of the oyster genus *Crassostrea* to better withstand high seston loads than the genus *Ostrea* (Yonge, 1936). However, no variation in these relative proportions was observed related to the turbidity gradients, suggesting that the ejection of waste material from the pallial cavity is not a functional constraint for *Crassostrea gigas* living in high SPM concentrations.

4.2. Pallial organ index and feeding functional thresholds

The mean annual SPM concentrations used to establish the quantitative relationship were obtained from hourly-recording *in situ* probes, which measured the different sources of variability (seasonal, fortnightly and semidiurnal tidal cycles) to provide an unbiased integrated measurement of the turbidity conditions experienced by feral oysters. The significant relationship obtained between G:P ratios and SPM concentrations therefore suggests that, in *Crassostrea gigas*, gill and palp variations allow feeding and ingestion volume regulation at high turbidities (Bernard, 1974; Foster-Smith, 1978; Widdows et al., 1979; Beninger et al., 2008). Indeed, the particle-processing capacities of oyster heterorhabdic gills have only been demonstrated at low numerical SPM concentrations and could be insufficient, without augmentation by palp particle sorting, to optimize food intake at high-turbidity conditions (Cognie et al., 2003; Beninger et al., 2008).

In bivalves, feeding constraints are commonly associated with functional thresholds of SPM concentrations, experimentally determined for particle retention (Palmer and Williams, 1980; Barillé et al., 1993), filtration (Barillé et al., 1997b; Navarro and Widdows, 1997; Velasco and Navarro, 2002) and selection (Pastoureaud et al., 1996; Barillé et al., 1997b; Navarro and Widdows, 1997). In oysters, some of these thresholds, such as the critical size of particles for entry into the openings of the gill principal filaments (Cognie et al., 2003) and particle retention in the gill interfilamentary spaces (Palmer and Williams, 1980; Barillé et al., 1993), have previously been directly related to the functionally heterorhabdic gill structure. During prolonged turbidity, the flexibility of the particle-processing surfaces of gills and palps could modify the functional thresholds and therefore the range of SPM concentrations tolerated by heterorhabdic bivalves. In high-turbidity conditions, this induces a physiological–morphological trade-off, as the energetic cost of pallial organ size variations is compensated by optimization of the food intake (DeWitt et al., 1998; Piersma and Drent, 2003; Bayne, 2004). Thus, the SPM concentration thresholds for the cessation of filtration (192 mg l^{-1}) and pre-ingestive selection (150 mg l^{-1}), determined for *Crassostrea gigas* living between IT and HT conditions (Barillé et al., 1997b), could change as a function of habitat turbidity. It is thus evident that cost–benefit analysis of oyster pallial organ plasticity must be considered in any study of oyster energetics and production, and most importantly especially for the development of ecophysiological models which seek to quantify energy budgets and population management in turbid environments (Barillé et al., 1997a; DeWitt et al., 1998; Ernande et al., 2004; Pouvreau et al., 2006; van der Veer et al., 2006).

Acknowledgements

The authors wish to thank the Groupement d'Intérêt Public (GIP) Loire Estuaire for the environmental data recorded in the Loire Estuary.

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