Spatial and temporal adjustments in gill and palp size in the oyster *Crassostrea gigas*

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ABSTRACT

Spatial and temporal variations in gill and palp size were studied during 1 year in naturally-settled populations of the Pacific oyster *Crassostrea gigas*, reciprocally transplanted between two contrasting sites located along a marked gradient of turbidity conditions. The variability of suspended particulate matter (SPM) and food particles, estimated by the concentration of chlorophyll-*a*, was measured with *in situ* water-quality probes. Over a full seasonal cycle, oysters exposed to high-turbidity (HT) conditions exhibited a lower gill-to-palp (G:P) ratio, compared with those exposed to low-turbidity (LT) conditions. Seasonal variations in the G:P ratio were observed at the LT site in relation to the spring phytoplanktonic bloom, but differed from those that had been observed previously. In fact, palp enlargement and gill narrowing (lower seasonal G:P ratio) suggest that oysters improved their pre-ingestive selection efficiency as a priority, rather than their filtering capacity. This result indicates that suspension-feeding bivalves do not have independent plastic responses of their foraging structures to either SPM quality or quantity, and that the direction of variations in the G:P ratio depends on the combination of these two factors. At the HT site, no seasonal pattern was observed in the G:P ratio. This can be explained by the strong hourly variations in SPM and chlorophyll-*a*, associated with tidal cycles, with daily variations that can be similar to those observed over a year. Reciprocal transplantations showed that oysters originating from the same site can differ in their feeding apparatus morphology when they grow in different environments and that temporal variations in the G:P ratio of oysters transplanted to a new environment converge towards that of individuals that have spent their entire life in this environment. Variations in the relative gill and palp sizes of *C. gigas* appear therefore to be partly the consequence of reversible phenotypic plasticity in response to spatial and temporal variations in SPM quantity and quality. The results also suggest that the limits and dynamics of gill and palp plasticity are dependent on the origin of oyster populations. Considering its role in the exploitation of different trophic conditions, and consequently in the biological performances (growth and reproduction), plasticity in the feeding apparatus morphology of *C. gigas* could be a determinant in the establishment of invasive populations in new ecosystems or in the management of farmed oysters.

INTRODUCTION

In coastal ecosystems, the re-suspension of bottom material by tidal currents and wind action leads to marked spatial and temporal variations in suspended particulate matter (SPM) quantity and quality (i.e. its relative composition in terms of food particles and other particles). This affects the availability of food, mostly microalgae, to suspension-feeding bivalves and thus their biological performance (Bayne *et al.*, 1987; Navarro *et al.*, 1992; Urrutia *et al.*, 1996; Barillé *et al.*, 1997; Navarro & Widdows, 1997). In these molluscs, gills and labial palps are the main pallial organs responsible for the capture and pre-ingestive processing of suspended particles (Shumway *et al.*, 1985; Prins *et al.*, 1991; Beninger *et al.*, 1992; Barillé, 1994; Ward & Shumway, 2004). The gills generate water currents in the pallial cavity and trap particles, which are then transferred to the labial palps. According to the gill structure, particle selection (i.e. the sorting of food particles from trapped particulate matter) and ingestion volume regulation occur either on the palps only or on both pallial organs, whose role is to improve the quality of the ingested ration by rejecting some particles outside the pallial cavity as pseudofaeces (Beninger & St-Jean, 1997; Beninger *et al.*, 1997; Ward *et al.*, 1998). In all cases, filtration rate and selection efficiency are closely dependent on the size of the particle-processing surfaces (Kiørboe & Møhlenberg, 1981; Jones *et al.*, 1992; Pouvreau *et al.*, 1999; Dutertre *et al.*, 2007; Compton *et al.*, 2008).

In marine and freshwater suspension-feeding bivalves, significant intraspecific differences in pallial organ size have been observed and related to turbidity level, i.e. local SPM concentration

(Theisen, 1982; Essink *et al.*, 1989; Payne *et al.*, 1995a, b; Barillé *et al.*, 2000; Dutertre *et al.*, 2007, 2009a; Yoshino *et al.*, 2012; Paolucci *et al.*, 2014). These morphological variations, generally resulting in smaller gills and larger palps at high-turbidity levels, prevent particulate matter from saturating the ciliated particle-processing surfaces and could therefore modify the range of SPM concentrations tolerated by bivalves (Dutertre *et al.*, 2007, 2009a). Considering bivalve pre-ingestive feeding behaviour as an integrated process (Foster-Smith, 1975, 1978; Milke & Ward, 2003; Ward *et al.*, 2003; Dutertre *et al.*, 2007), the gill-to-palp area (G:P) ratio is a sensitive turbidity-related indicator commonly used to describe the functional association of these two pallial organs (Payne *et al.*, 1995b; Honkoop *et al.*, 2003; Drent *et al.*, 2004; Compton *et al.*, 2007; Dutertre *et al.*, 2009a). Although some signs of genetic differentiation between populations have also been detected (Drent *et al.*, 2004), intraspecific variations in the G:P ratio of bivalves exposed to both spatially (Essink *et al.*, 1989; Drent *et al.*, 2004; Dutertre *et al.*, 2009a) and temporally (Honkoop *et al.*, 2003) varying environmental conditions have mostly been attributed to phenotypic plasticity, a common strategy observed in sessile organisms, including most of the suspension-feeding bivalves, which are entirely dependent on local resources (Pigliucci, 2001).

The Pacific cupped oyster, *Crassostrea gigas* (Thunberg, 1793) is a worldwide, economically-important, suspension-feeding bivalve introduced—and now invasive—in several coastal ecosystems (Diederich *et al.*, 2005; Ruesink *et al.*, 2005). In this species, in which particle selection and ingestion-volume regulation occur on both gills and palps, the ability to proliferate in temperate turbid ecosystems was recently related to size variations in these two feeding organs (Dutertre *et al.*, 2007, 2009a), by establishing a significant quantitative relationship between spatial variations of annual mean SPM concentration and G:P ratio. In order to understand fully the feeding strategy of oysters in such ecosystems, where they are exposed to both seasonal and tidal variations in environmental conditions, the present study explored the temporal variations in their G:P ratio and the limits of phenotypic plasticity (DeWitt *et al.*, 1998; Honkoop *et al.*, 2003). Naturally-settled oysters were reciprocally transplanted between two contrasting sites located along a marked turbidity gradient in order to assess variations in their G:P ratio over a full seasonal cycle together with their growth performances. Variations in G:P ratio and growth performances are discussed in relation to the real-time monitoring of the variability in the quantity and quality of SPM and food particles, estimated from hourly data obtained from *in situ* probes.

MATERIAL AND METHODS

Reciprocal transplantation design and sampling scheme

In March 2005, oysters naturally settled on hard substrata were collected from two sites, 15 km apart, located along a marked gradient of SPM concentration in Bourgneuf Bay, France (Haure & Baud, 1995; Dutertre *et al.*, 2009a; Fig. 1). The northern site (La Coupelasse, 47° 1′ 34.7″N, 2° 1′ 55.9″W) is a mudflat (more than 44% of the total weight of the sediment corresponds to a size fraction <44 μm) with a highly turbid (HT) water column, whereas the southern site (Gresseloup, 46° 57′ 2.6″N, 2° 7′ 53.4″W) has a coarser granulometry (<10% of the total weight of the sediment corresponds to a size fraction <44 μm) with lower turbidity (LT) levels in the water column. Oysters from each site were separated into two batches of 380 individuals. One batch was left at the native site and the other was transplanted to the other site in order to be exposed to new turbidity conditions. Transplanted and native oysters, placed in plastic mesh bags and tied on oyster racks at 60 cm above the bottom, were then sampled ($n = 20$) regularly during 1 year.

On each sampling date, oysters were transferred to the laboratory, manually cleaned of their epibionts and sediment, and dried
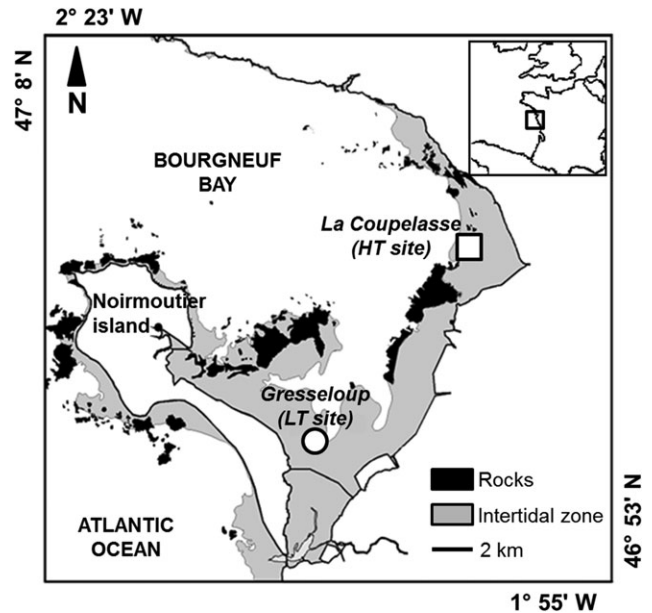

Figure 1. Location of the two experimental sites in Bourgneuf Bay. La Coupelasse is the high-turbidity (HT) site and Gresseloup the low-turbidity site (LT).

with absorbent paper. Individuals were weighed to determine their total mass (TM, g) before their valves were opened. The right valve was then removed and digital photographs were taken (Nikon Coolpix 995) of the right outer lamella of the right gill and the right outer palp. Their respective areas (cm^2) were delineated and calculated with the image-analysis software LUCIA G v. 4.80 (Image Analysis Systems). Finally, all soft parts were collected and dried at 60 °C for 48 h to obtain the dry tissue mass (DTM, g) of individuals.

Dry tissue mass was used to standardize gill and palp areas according to the following equation (Bayne *et al.*, 1987):

$$\Upsilon_{stand} = (1/DTM)^b \times \Upsilon_{obs}$$

where Υ_{stand} and Υ_{obs} are the standardized and observed organ areas, respectively, and b is the exponent in the allometric relationship $\Upsilon = aDTM^b$ relating oyster gill or palp area to their dry tissue mass at the HT and LT sites, as determined by Barillé *et al.* (2000). This standardization procedure amounts to considering pallial organ areas for individuals with a dry tissue mass normalized to 1 g. The G:P area ratio (standardized gill area/standardized palp area) was then used to compare pallial organ size variations (Dutertre *et al.*, 2009a).

Environmental parameters

Multi-parameter water quality probes (YSI 6,600) were fixed to oyster racks installed at each sampling site, to record daily nephelometry (NTU) and fluorometry (%). SPM and chlorophyll-*a* (chl-*a*) concentrations were then estimated from these records using the following calibration procedure.

Field calibrations were performed using probe records and natural seawater samples (four replicates per sample) collected simultaneously every 3 h at each oyster sampling site over two semi-diurnal tidal cycles. Half of the seawater replicates were dried at 60 °C for 48 h and then ashed at 450 °C for 4 h (Barillé-Boyer *et al.*, 2003) to obtain SPM concentrations, while the other replicates were analysed by spectrophotometry after extraction with acetone (Lorenzen, 1967) to determine chl-*a* concentration, which was used as a food quantifier. Hourly probe records were then

transformed into SPM (mg l^{-1}) and chl-*a* (µg l^{-1}) concentrations, based on linear regression equations relating SPM to nephelometry and chl-*a* to fluorometry, respectively. Details of the calculation were given by Dutertre *et al.* (2010).

Statistical analysis

Paired *t*-tests were performed on SPM and chl-*a* concentrations to assess whether they differed between sites, while the relationship between these two environmental variables was examined through Pearson correlations at each site. Sources of variation in pallial organ size and individual body growth were analysed by performing three-way analyses of variance (ANOVAs) on biometric measurements (G:P ratio, gill area, palp area, TM and DTM) with rearing site (LT *vs* HT site), origin of population (LT *vs* HT population), date (months) and their interactions as explanatory factors. The normality of the residuals was checked using the Shapiro–Wilk test (Shapiro & Wilk, 1965) and homoscedasticity was assessed by visual inspection of the residuals plotted against the predicted values. No evidence of autocorrelation or partial autocorrelation was found in the ANOVA residuals, which therefore complied with the independence assumption of linear models. Type III *F*-tests were used to evaluate the significance of the effects (Fox & Weisberg, 2011) while partial η^2 was used as a measure of effect size. When appropriate, Student–Newman–Keuls (SNK) tests were then carried out *a posteriori* to determine which factor levels differed from the others. Analyses were performed with the statistical software R v. 3.3.0.

RESULTS

Spatio-temporal variability in quantity and quality of suspended particulate matter

From March 2005 to February 2006, SPM concentration differed between LT and HT sites (Fig. 2A, C, paired *t*-test, $n = 365$, $t = -19.75$, $P < 0.01$), with a significantly higher annual mean at the HT site (125.40 ± 96.38 (SD) mg l^{-1} *vs* 26.83 ± 24.94 mg l^{-1}). At the HT site, SPM concentration varied from 5.87 mg l^{-1} to 558.34 mg l^{-1}, with 75% of the daily values higher than 59.17 mg l^{-1}. In contrast, at the LT site, SPM concentration varied from 7.46 mg l^{-1} to 240.71 mg l^{-1}, with 75% of the daily values lower than 34.18 mg l^{-1}. No seasonal pattern was observed at the HT site, whereas a peak of turbidity was detected in autumn at the LT site, probably in relation to dredging activities at a nearby harbour.

Chl-*a* concentration also differed significantly between sites (Fig. 2B, D, paired *t*-test, $n = 365$, $t = -25.69$, $P < 0.01$), being higher at the HT site (7.99 ± 4.16 µg l^{-1} *vs* 2.33 ± 2.05 µg l^{-1}). At the HT site, chl-*a* concentration varied from 1.65 µg l^{-1} to 24.26 µg l^{-1}, with 75% of the daily values higher than 4.77 µg l^{-1}. In contrast, at the LT site, chl-*a* concentration varied from 0.31 µg l^{-1} to 17.30 µg l^{-1}, with 75% of the daily values lower than 2.87 µg l^{-1}. Chl-*a* concentration clearly increased in spring (April–May) at the LT site, whereas no seasonal pattern was apparent at the HT site. Variations in SPM concentration and chl-*a* concentration were positively correlated at both sites (Pearson correlation test), with a stronger correlation at the HT site ($r = 0.83$, $P < 0.01$) compared with the LT site ($r = 0.17$, $P < 0.01$).

Sources of variation in pallial organ size

The G:P ratio differed significantly between rearing sites (Table 1: Site, partial $\eta^2 = 0.21$, $P < 0.01$) being on average larger at the LT site (5.37 ± 0.78) than at the HT site (3.03 ± 0.10) (Fig. 3A, B). However, it also differed significantly according to the origin of the population (Table 1: Origin, partial $\eta^2 = 0.09$, $P = 0.02$) with greater values in the LT population (4.91 ± 0.82) than in the HT population (3.65 ± 0.84). In fact, temporal patterns of G:P ratio variation of transplanted oysters became significantly different from those observed in their original site (SNK-tests between Sites for each Origin on different Dates, $P < 0.01$). These differences
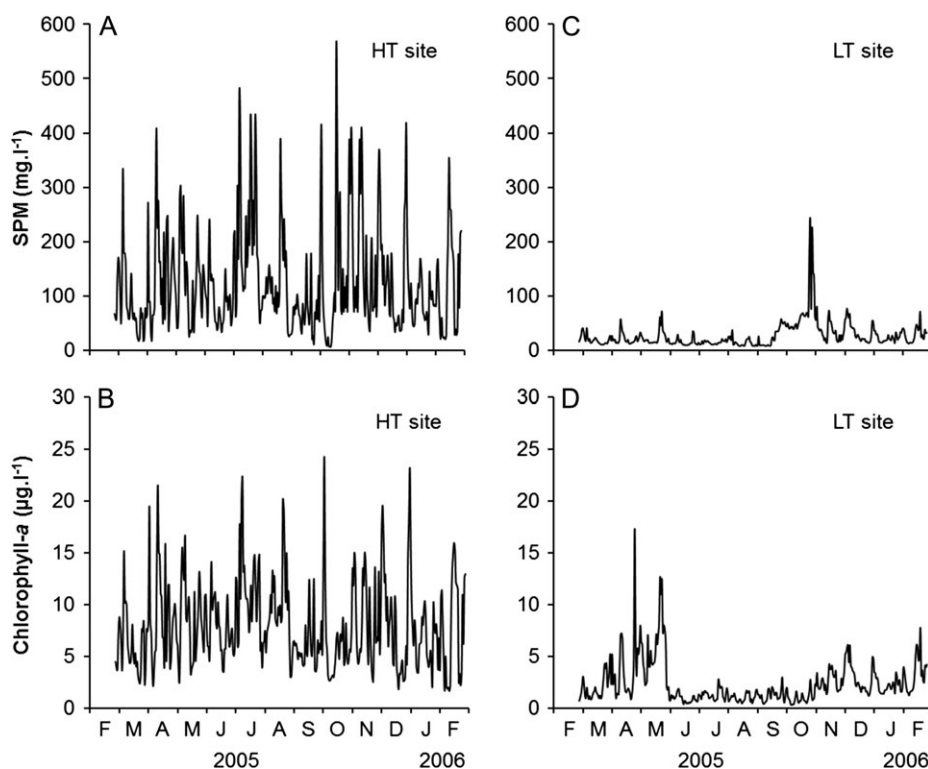

Figure 2. Daily variations in suspended particulate matter (SPM) and chlorophyll-*a* concentrations at the high-turbidity (HT, **A** and **B**) and low-turbidity (LT, **C** and **D**) sites in Bourgneuf Bay.

Table 1. Sources of variation in pallial organ size and body growth.

Trait	Source of variation	df	F	Partial η^2	P
G:P ratio	Site	1	15.75	0.21	<0.01
	Origin	1	74.94	0.09	0.02
	Date	9	0.55	0.00	0.80
	Site × Origin	1	1.07	0.23	0.33
	Site × Date	9	6.14	0.12	<0.01
	Origin × Date	9	1.65	0.02	0.23
	Site × Origin × Date	9	1.78	0.04	0.07
	Residual error	742			
Gill area	Site	1	4.73	0.05	0.13
	Origin	1	6.81	0.00	0.36
	Date	9	8.21	0.44	0.01
	Site × Origin	1	0.79	0.02	0.40
	Site × Date	9	1.96	0.09	0.16
	Origin × Date	9	0.89	0.05	0.56
	Site × Origin × Date	9	4.15	0.04	<0.01
	Residual error	742			
Palp area	Site	1	7.39	0.19	0.12
	Origin	1	14.20	0.02	0.13
	Date	9	3.82	0.33	0.02
	Site × Origin	1	6.41	0.24	0.03
	Site × Date	9	3.74	0.10	0.03
	Origin × Date	9	1.70	0.03	0.22
	Site × Origin × Date	9	2.33	0.05	0.01
	Residual error	742			
TM	Site	1	11.83	0.08	0.02
	Origin	1	1.68	0.00	0.33
	Date	9	8.90	0.39	<0.01
	Site × Origin	1	1.83	0.01	0.21
	Site × Date	9	5.32	0.06	0.01
	Origin × Date	9	1.85	0.01	0.18
	Site × Origin × Date	9	0.96	0.02	0.47
	Residual error	742			
DTM	Site	1	13.80	0.13	<0.01
	Origin	1	0.33	0.00	0.58
	Date	9	3.69	0.35	0.01
	Site × Origin	1	0.39	0.00	0.54
	Site × Date	9	20.59	0.09	<0.01
	Origin × Date	9	7.97	0.01	<0.01
	Site × Origin × Date	9	0.41	0.04	0.92
	Residual error	742			

Type III *F*-tests of the three-way ANOVAs on gill-to-palp (G:P) ratio, gill area, palp area, total mass (TM) and dry tissue mass (DTM). Explanatory factors are rearing Site (low-turbidity LT *vs* high-turbidity HT site), Origin (LT *vs* HT population), Date (months) and their interactions.

appeared from May for HT oysters transplanted to the LT site, and from June for LT oysters transplanted to the HT site. Although the G:P ratio of native and transplanted oysters tended to converge within each site (Fig. 3), it remained significantly different overall (SNK-tests between Origins for each Site on different Dates, $P < 0.01$). Moreover, the G:P ratio exhibited temporal variations that differed between sites (Table 1: Site × Date, partial $\eta^2 = 0.12$, $P < 0.01$). Notably, it decreased in April to May at the LT site (SNK-tests, $P < 0.01$), whereas it showed no significant temporal variation at the HT site (SNK-tests, $P > 0.05$).

In contrast to gill area, palp area exhibited an origin-specific pattern of variation across sites (Table 1: Site × Origin, partial $\eta^2 = 0.02$ and $P = 0.40$ for gill area, partial $\eta^2 = 0.24$ and $P = 0.03$ for palp area) and a site-specific pattern of variation (Site × Date, partial $\eta^2 = 0.09$ and $P = 0.16$ for gill area, partial

$\eta^2 = 0.10$ and $P = 0.03$ for palp area). This suggests that morphological variation across sites was more pronounced in palp area than in gill area, with different amplitudes according to the population origin, and that palps were responsible for the site-specific temporal patterns of variation in G:P ratio. In fact, palp area was significantly larger at the HT site throughout the study, while gill area only showed significant differences between October and March. During this period, gill area was significantly higher at the LT site. An overall pattern of temporal variation in gill and palp areas was observed (Table 1: Date, partial $\eta^2 = 0.44$ and $P = 0.01$ for gill area, partial $\eta^2 = 0.33$ and $P = 0.02$ for palp area), but this was not the case for the G:P ratio (partial $\eta^2 = 0.09$, $P = 0.80$), suggesting that temporal variations in pallial organ size compensated for each other overall.

Sources of variation in body growth

Total mass (TM) and dry tissue mass (DTM) differed significantly between rearing sites (Table 1: Site, partial $\eta^2 = 0.08$ and $P = 0.02$ for TM, partial $\eta^2 = 0.13$ and $P < 0.01$ for DTM), both being on average larger at the LT site (60.3 ± 15.9 g for TM and 1.5 ± 0.4 g for DTM) than at the HT site (50.8 ± 9.6 g for TM and 1.1 ± 0.2 g for DTM). Moreover, temporal patterns in TM and DTM experienced a significant date effect (Table 1: Date, partial $\eta^2 = 0.39$ and $P < 0.01$ for TM, partial $\eta^2 = 0.35$ and $P = 0.01$ for DTM) and clearly differed between rearing sites (Table 1: Site × Date, partial $\eta^2 = 0.06$ and $P = 0.01$ for TM, partial $\eta^2 = 0.09$ and $P < 0.01$ for DTM). Body growth therefore appeared faster at the LT site than at the HT site (Fig. 4). Growth pattern also depended on the origin of individuals for DTM, but not for TM (Table 1: Origin × Date, partial $\eta^2 = 0.01$ and $P < 0.01$ for DTM, partial $\eta^2 = 0.01$ and $P = 0.18$ for TM), For example, irrespective of the rearing site, native oyster growth was faster than in transplanted individuals in terms of DTM (SNK-tests, $P < 0.01$) and TM (SNK-tests, $P < 0.01$ and $P = 0.19$, respectively). This was also revealed by differences after one year of increases in DTM (Fig. 4C, D, + 247% *vs* + 176% at LT site, + 130% *vs* + 112% at HT site), but also in TM, despite the non-significant effect (Fig. 4A, B, + 125% *vs* + 98% at LT site, + 45% *vs* + 38% at HT site).

DISCUSSION

Feeding apparatus morphology and trophic conditions

Over a full seasonal cycle, the average G:P ratio of *Crassostrea gigas* oysters experiencing LT conditions was systematically larger than that of individuals experiencing HT conditions. This result is consistent with the general pattern previously established for suspension-feeding bivalves: small gills and large palps are associated with high SPM concentrations (Theisen 1977, Essink *et al.*, 1989; Payne *et al.*, 1995a, b; Barillé *et al.*, 2000; Dutertre *et al.*, 2007, 2009a; Yoshino *et al.*, 2012; Paolucci *et al.*, 2014). Under a high SPM load, when food particles are diluted in abundant resuspended fine sediment, the association of large palps and small gills, corresponding to a low G:P ratio, allows a simultaneous increase in filtration rate and pre-ingestive particle selection efficiency, and therefore improves the quality of the ingested ration (Dutertre *et al.*, 2007). On the other hand, in LT environments, the dilution of organic particles by inorganic material is reduced as well as the total SPM load, and large palps are thus not required for particle selection and ingestion regulation. Concomitantly, high filtration rates enabled by large gills maximize food intake, leading to a larger G:P ratio. The G:P ratio was therefore expected to increase with food abundance relative to total SPM load, both across environments (Drent *et al.*, 2004) and across seasons, especially during
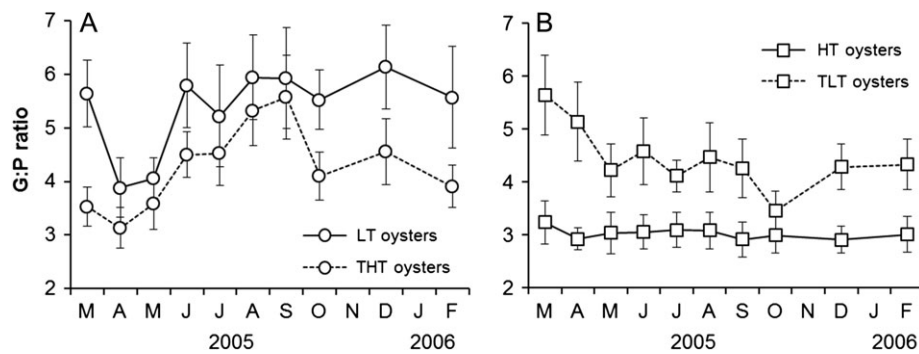
Figure 3. Variations in the gill-to-palp (G:P) ratio of the oyster *Crassostrea gigas* at the low-turbidity (LT, **A**) and high-turbidity (HT, **B**) sites of Bourgneuf Bay from March 2005 to February 2006. LT and HT oysters correspond to the native nontransplanted individuals from each site. THT oysters correspond to the individuals transplanted from the HT to the LT site at the beginning of the study, while TLT oysters correspond to the individuals transplanted from the LT to the HT site. Mean values are given with their 95% confidence intervals.
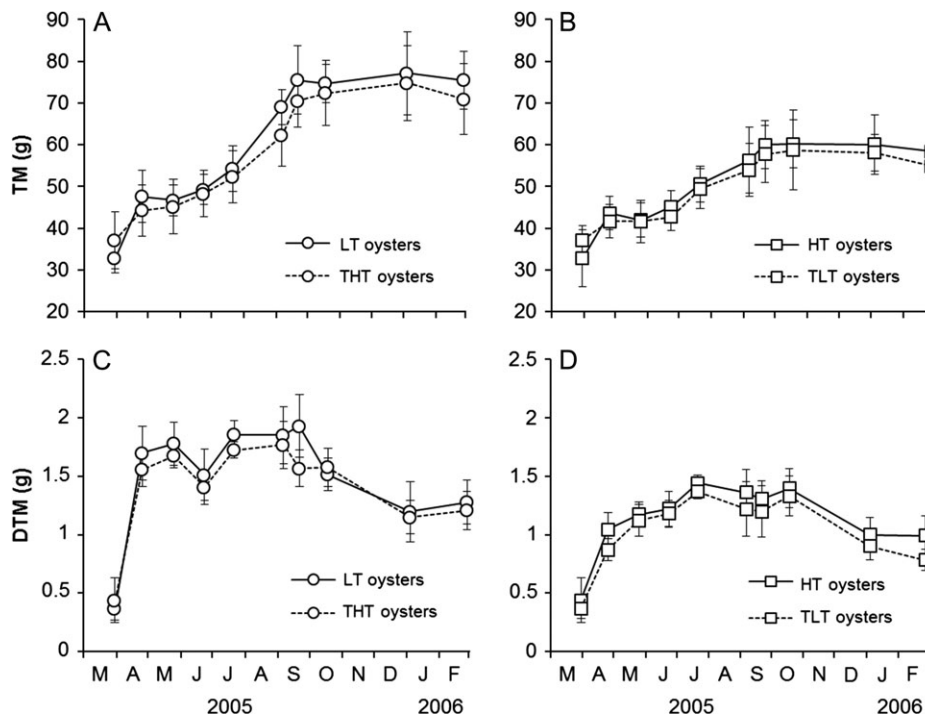

Figure 4. Variations in total mass (TM, **A** and **B**) and dry tissue mass (DTM, **C** and **D**) of the oyster *Crassostrea gigas* at the low-turbidity (LT) and high-turbidity (HT) sites of Bourgneuf Bay from March 2005 to February 2006. LT and HT oysters correspond to the native nontransplanted individuals from each site. THT oysters correspond to the individuals transplanted from the HT to the LT site at the beginning of the study, while TLT oysters correspond to the individuals transplanted from the LT to the HT site. Mean values are given with their 95% confidence intervals.

periods of phytoplankton bloom (Honkoop *et al.*, 2003; Piersma & Drent, 2003).

The seasonal pattern of plastic variation in the feeding apparatus morphology of oysters was opposite to what has previously been anticipated in response to seasonal variability in food availability (Honkoop *et al.*, 2003; Piersma & Drent, 2003). In LT conditions, the G:P ratio exhibited a marked reversible decrease in spring, which was concomitant with the phytoplanktonic bloom as indicated by a sharp increase in chl-*a* concentration, while total SPM load remained unchanged. During this period, simultaneous palp enlargement and gill narrowing suggest that oysters improved their pre-ingestive selection efficiency (Dutertre *et al.*, 2007), probably in order to optimize the exploitation of the phytoplankton bloom in spring. For example, the blooming diatom *Leptocylindrus minimus*, detected in Bourgneuf Bay (Hernández-Fariñas, 2015) and nonedible for *C. gigas* (Alunno-Bruscia *et al.*, 2011), forms large chains that can likely be processed only on the palps (Cognie *et al.*,

2003). Such an optimization of food intake by means of seasonal morphological plasticity could explain why oysters at the LT site grew faster (this study) and reproduced more intensively (Dutertre *et al.*, 2009b) than the HT oysters during spring. We suggest that the foraging structures of suspension-feeding bivalves do not have independent plastic responses to both SPM quality and quantity, and that the direction of variations in the G:P ratio depends on the combination of these two factors. However, the respective roles of SPM quality and quantity in determining gill and palp variations can hardly be evaluated quantitatively in natural conditions, since these two factors generally covary (in HT conditions for example; see below). A controlled experiment with a design across gradients of both food abundance and turbidity would be more appropriate (Drent *et al.*, 2004).

In HT conditions, no seasonal pattern of plastic variation in the G:P ratio was observed. At the HT site, the abundant fine mud particles are more easily resuspended by water movements,

inducing high-amplitude short-term SPM variations mainly linked to the semi-diurnal tidal cycle and wind action (causing waves or swell). Thus, during the few hours of a spring tidal cycle, organisms can be exposed to a range of SPM concentrations similar to those observed over an entire year. The associated resuspension of microphytobenthos (benthic microalgae) biomass, highlighted by the strong correlation between chl-*a* and SPM variations, constitutes an important food supply, which may hide the seasonal phytoplankton events. This effect resulted in food abundance, indicated by chl-*a* concentration, being systematically higher at the HT site but, like the total SPM load, without exhibiting any seasonal variability, thus explaining the absence of seasonal plastic variations in feeding-apparatus morphology. Moreover, under such strong short-term variability, corresponding short-term changes in the G:P ratio would not be advantageous with regard to the costs and benefits of pallial-organ plasticity and/or might be limited by the morphological response time (DeWitt *et al.*, 1998; Bayne, 2004; Ernande & Dieckmann, 2004). The absence of seasonal adjustments in the G:P ratio, and consequently in pre-ingestive particle processing, could partly explain the slower growth observed in HT conditions (Haure & Baud, 1995; Dutertre *et al.*, 2009b and this study).

Limits and polymorphism of phenotypic plasticity

The transplantation experiment shows that oysters originating from the same site can differ in their feeding apparatus morphology when they grow in different environments. Moreover, temporal variations in the G:P ratio of oysters transplanted to a new environment converge towards that of individuals that have spent their entire life in this environment. As observed in other bivalves (Essink *et al.*, 1989; Drent *et al.*, 2004), variations in the G:P ratio of *C. gigas* appear therefore to be partly the consequence of reversible phenotypic plasticity in response to spatial and temporal variations in SPM quantity and quality. Within each site, the similarities in TM and DTM variations of native and transplanted oysters probably reflect the maximum growth performances resulting from behavioural and/or physiological adjustments associated with local turbidity conditions, including the optimization of the food intake induced by plastic variations in gill and palp size.

In spite of the plastic convergence in the feeding apparatus morphology of oysters from different origins exposed to the same environment, the G:P ratio of the transplanted individuals never reached the same values as the native ones in either LT or HT conditions. These results suggest origin-dependent limits of phenotypic plasticity corresponding to a polymorphism across populations in feeding apparatus morphology. It remains an open question whether this is related to the fact that they already have a constitutive lower G:P ratio, but nevertheless the observed polymorphism across populations could induce a lower capacity of transplanted oysters than native individuals to deal with local trophic conditions. The resulting disadvantage in terms of food intake could explain the systematically slower growth of transplanted oysters within each site. Given that total tissue mass includes soma, reserves and gonads, and thus is positively related to fecundity (Ernande *et al.*, 2004), and that smaller individuals are more likely to suffer predation mortality as observed for several bivalves (Nakaoka, 1996; Smith & Jennings, 2000), the disadvantage of transplanted individuals in terms of growth performance most probably translates into a disadvantage in terms of fecundity and survival, suggesting a real fitness advantage for native oysters in their own environment.

CONCLUSION

In this study, the Pacific oyster *Crassostrea gigas* exhibits reversible plastic variations in the G:P ratio, which appear to be related to spatial and temporal variations in SPM quantity and quality. Considering that the pre-ingestive particle processing—especially filtration rate and particle selection efficiency (Kiørboe & Møhlenberg, 1981; Dutertre *et al.*, 2007)—of oysters is closely dependent on gill and palp size, these morphological variations may have consequences for various energetic requirements, including somatic growth, reproduction or immune response. Polymorphism in gill and palp size variation between native and transplanted organisms also suggests that the limits and dynamics of feeding-organ plasticity could be a determinant in the establishment of invasive populations in new ecosystems (Dybdahl & Kane, 2005), or in the management of farmed oysters, which are regularly transplanted during their life cycle in order to maximize biological performances (Dumbauld *et al.*, 2009).

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