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Rising water temperatures, reproduction and recruitment of an invasive oyster, *Crassostrea gigas*, on the French Atlantic coast

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ABSTRACT

The recent appearance and invasion of feral oysters (*Crassostrea gigas*) along the northern European Atlantic coast, underscores the necessity to investigate the relationship between environmental variables, reproductive physiology, larval development and recruitment. We studied these relationships at both high (HT) and intermediate (IT) – turbidity sites, through historical data on water temperatures, multi-parameter environmental probes, histological analyses, and field collections of planktonic larvae and settled post-larvae in 2005 and 2006. A progressive warming trend was observed, especially since 1995, when oyster proliferation first became severe. Threshold temperatures for oocyte growth, larval development and settlement were achieved in both 2005 and 2006. The HT site showed greater numbers of larvae and post-larvae than the IT site for both years, with the highest numbers of post-larvae observed at both sites during the warmer summer of 2006. These results suggest that increased temperatures in northern European waters allow successful reproduction, larval development, and recruitment of *C. gigas*. High turbidity conditions further enhance this success.

1. Introduction

Suspension-feeding bivalves are coastal ecosystem engineers that regulate matter and energy fluxes by coupling pelagic and benthic processes (see Dame and Olenin (2005) for reviews). In the 20th century, over-exploitation, pollution, and disease led to a worldwide decline in native oyster populations, accompanied by economic losses and ecological changes (Newell, 1988; Quayle, 1988; Ruesink et al., 2005). The Pacific cupped oyster, *Crassostrea gigas*, was voluntarily introduced in several new coastal areas around the world for aquaculture purposes, because of its rapid growth rate, high tolerance to environmental variations and low susceptibility to oyster diseases (Coleman, 1986; Smith et al., 1986; Grizel and Héral, 1991).

Although successful introductions of *C. gigas* occurred particularly in northern temperate countries of Europe and North America, water temperatures precluded substantial larval recruitment in the northernmost regions (Le Borgne et al., 1973; Gruet et al., 1976; Goulletquer, 1995; Drinkwaard, 1999). France is a particularly interesting case, since the occurrence of massive and regular feral *C. gigas* recruitments in the southern Atlantic regions, but not in the northern ones, suggested that the limit for the successful larval development was situated south of Bourgneuf Bay (Goulletquer and Héral, 1991; Robert and Gérard, 1999). However, in the past decade, feral oysters have proliferated on northern European Atlantic coasts, unrelated to new introductions, and *C. gigas* is now considered to be an invasive organism from Spain to the North Sea (Reise et al., 1999; Wehrmann et al., 2000; Cognie et al., 2006; Brandt et al., 2008). This phenomenon is particularly visible in northern French turbid bays, where the feral *C. gigas* build long-lasting reefs and colonize racks on which are attached farmed *C. gigas* bags (Martin et al., 2004, 2005). In these areas, trophic competition with feral oysters has been suggested to explain the decline in farmed oyster growth performance in the last 10 years (Cognie et al., 2006). Although reproduction performances of farmed adult oysters are being elucidated (Dutertre et al., in press), field studies on natural recruitment are also necessary to understand the recent feral oyster invasion (Underwood and Fairweather, 1989; Grosberg and Levitan, 1992; Smaal et al., 2005).

Optimal larval development of *C. gigas* requires a water temperature higher than 22 °C during at least two weeks (Arakawa, 1990; Shatkin et al., 1997; Rico-Villa et al., 2008) and oyster larvae are affected by food quality and quantity (Baldwin and Newell, 1995; Powell et al., 2002; Rico-Villa et al., 2008). As larval survival is the determining element for the settlement of feral oyster populations (Gosling, 2003), environmental influences on larval development need to be clarified by field studies, especially in turbid

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coastal waters which are characterized by seasonal and short-term variations of the environmental conditions (Mann, 1982).

In an attempt to determine the causes of the recent invasion of feral oysters, in northern cold temperate ecosystems, the present study analyzed the larval development and post-larval recruitment of *C. gigas* at the southern and northern geographic extremes of Bourgneuf Bay in relation to real-time monitored environmental factors.

2. Materials and methods

2.1. Adult oyster sampling and tissue fixation

Feral and farmed oysters were collected at two oyster-farming sites in Bourgneuf Bay, between February 2005 and July 2006 (Fig. 1, Haure and Baud, 1995). The northern site, La Coupelasse (47°1′34.7″N, 2°1′55.9″W), is a high-turbidity mudflat compared to the southern sandy-muddy bottom site, Gresseloup (46°57′2.6″N, 2°7′53.4″W).

At the beginning of the study, in February 2005, adult farmed oysters (shell length = 69.2 ± 4.9SD mm, originating from 18-month hatchery-born spats), were installed, at both the northern and southern sites, in 1.0 × 0.5 m plastic, 20 mm mesh bags and tied to oyster racks (3.0 × 1.0 m) at 0.6 m above the bottom. Each bag contained 280 individuals, corresponding to 5–10 kg of oysters. At each site, 15 farmed and 15 feral oysters were then sampled once monthly until March 2006 and then twice monthly until July 2006. Feral oysters, in the same range of shell length as farmed ones, were collected near oyster racks on fixed substrata. For each oyster, shell dimensions (length, width and height) were measured with a caliper and whole mass was determined before shucking. Soft tissues were then immediately fixed in cold aqueous Bouin's solution (approx. 5 × animal volume) for at least two weeks (Beninger et al., 2001).

2.2. Histological preparation

After fixation, a 0.5 mm-thick slice of the visceral mass was removed from the region along the line connecting the left and right palp-gill junctions (Morales-Alamo and Mann, 1989). The tissue was rinsed under running water overnight to eliminate excess Bouin's solution, dehydrated and prepared for paraffin embedding. Embedded tissues were sliced with a microtome to obtain 10 histological sections per individual, 7 μm in thickness. These sections were rehydrated, stained with modified Masson's trichrome and dehydrated before being mounted on glass slides in mounting medium (Beninger et al., 2001). Mounted histological sections were then dried at 60 °C for at least one week.

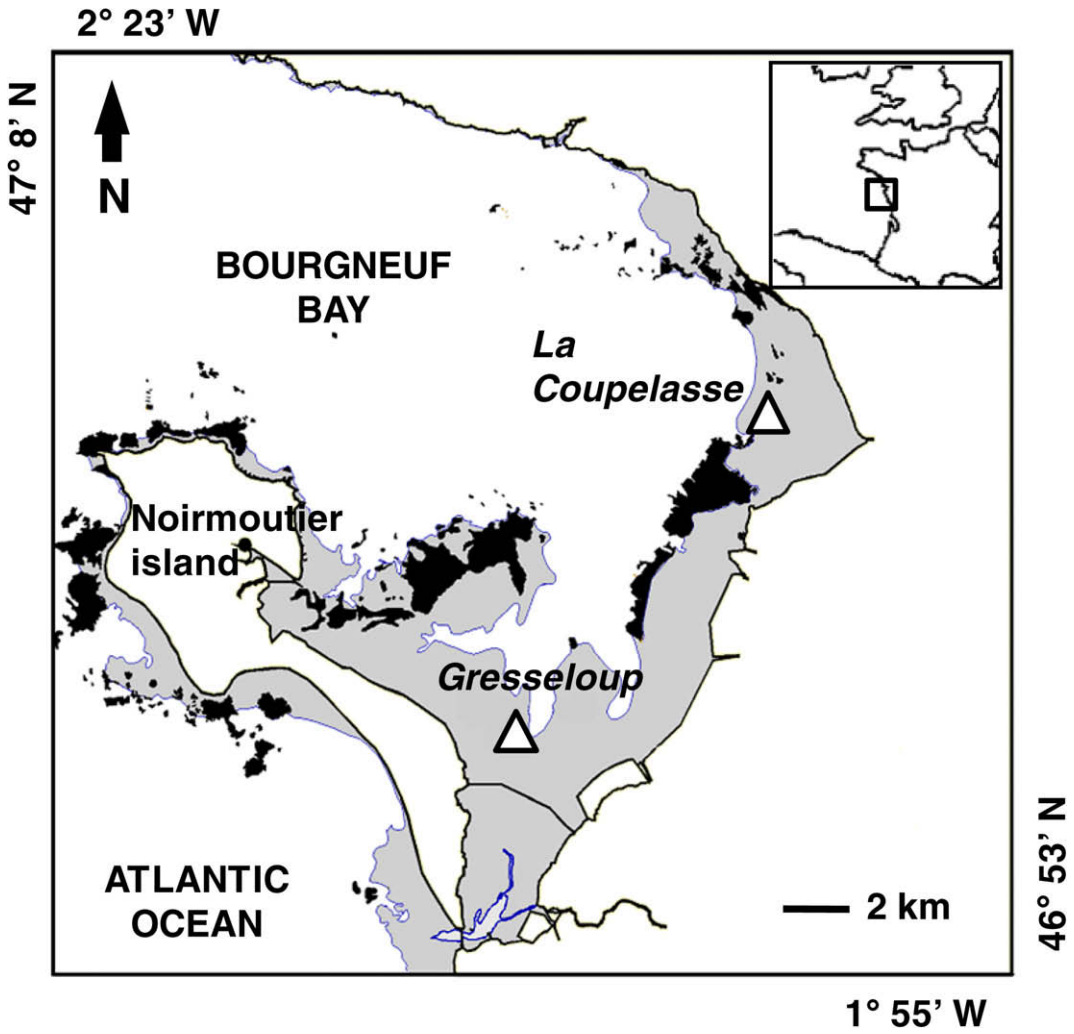

Fig. 1. Location of northern (La Coupelasse) and southern (Gresseloup) oyster sampling sites (△) in Bourgneuf Bay. The intertidal zone and rocks are represented by gray and black areas, respectively (modified from Barillé et al. (2000)).

2.3. Microscopic determinations and oocyte size measurements

Oyster larvae are characterized by an initial endotrophic stage (utilization of stored oocyte reserves), followed by a mixotrophic stage (oocyte reserves + ingested particles) and finally an exotrophic stage (ingested particles only – Lucas et al., 1986; His and Seaman, 1992; Cannuel and Beninger, 2005). Oocytes increase in size during vitellogenesis, so the relative amount of oocyte reserves was therefore estimated by measuring oocyte sizes in histological sections of female oysters, observed on a computer screen connected to a video camera (Nikon DXM 1200F) and optical microscope (Olympus AX70). LUCIA 4.80 software (Image Analysis Systems) was used to measure oocyte area showing sections passing through both the clear nucleus and a least one nucleolus (n = 30/oyster). Oocyte diameter was then calculated as follows:

$$\text{Oocyte diameter } (\mu\text{m}) = 2 \times \sqrt{(\text{oocyte area } (\mu\text{m}^2)/\pi)}$$

Monthly means (±95% confidence intervals, CI) of oocyte diameters were calculated and used to determine the gonadal development stage (Lango-Reynoso et al., 2000): early gametogenesis (3.0–12.0 μm), growing (12.1–30.0 μm), mature (30.1–41.0 μm) or atretic (41.1–60 μm).

2.4. Determinations of D-larva and post-larval densities

Unambiguous identification of *C. gigas* larvae was achieved through a preliminary inventory of larval bivalve species at the two study sites, followed by identification using literature data (Rees, 1950; Le Pennec, 1978; His, 1991) and computer image analysis of key shell characteristics (Lucia G 4.80 software).

During known oyster spawning periods, plankton samples were collected at the northern and southern sites using a boat-mounted pump provided with a flowmeter. Each plankton sample (1.5 m^3) was fixed in 10% formaldehyde–seawater solution and prepared for analysis as in Auby et al. (2002). Each sample was manually homogenized with a loop-ended glass stick to avoid damage to larvae, and two 0.5 ml aliquots were transferred to Sedgewick–Rafter counting cells and observed using a light microscope (Olympus AX70) in order to determine D-larva densities (shell height = 57–105 μm; Rees, 1950; Le Pennec, 1978; His, 1991).

At each site, clusters of 10 striated tubular collectors (commonly used as substrata for oyster spat settlement in the field; length = 120 cm, diameter = 2 cm) were tied side by side to oyster racks (3.0 × 1.0 m) at 0.6 m from the bottom. The clusters were rolled up at the end of each tidal cycle to count the post-larval (i.e., recently-settled spats) density, and replaced with new clusters for the next tidal cycle.

2.5. Environmental monitoring

Multi-parameter water quality probes (YSI 6600) were fixed to oyster racks installed at each sampling site, to record temperature (°C), salinity (from conductivity), suspended particulate matter (SPM) concentration (nephelometry, NTU) and chlorophyll-*a* (chl-*a*) concentration (fluorometry, %) every hour. The corresponding monthly means were plotted with their 95% confidence intervals (n = 720).

Food is implicitly defined as ingestible matter. Since we do not know what, precisely, the oysters are ingesting, we can only use indicators of available food. These must take into account:

Quantity:
Suspended particulate matter – the total amount of particles, quality not specified.
Particulate organic matter (POM) – potentially digestible particles, but quality not specified.
Chlorophyll-*a* – amount of available phytoplankton, proportion of the available particulate matter not specified.
Quality:
POM:SPM – an indication of the organic content of the SPM (dilution of POM).
Chl-*a*:POM – an indication of the quality of the organic matter.

In order to characterize potential food amount, availability, and quality, field calibrations for suspended matter were performed simultaneously from both probe records and natural seawater samples collected at each oyster sampling site over two tidal cycles. Some seawater samples (n = 17) 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 and POM concentrations (mg l^{-1}), respectively, while other samples (n = 16) were analyzed by spectrophotometry after extraction with acetone (Lorenzen, 1967) to determine chl-*a* concentrations (μg l^{-1}). Linear regressions obtained from field samples were used to transform hourly probe records into concentrations as follows:

$$\text{SPM } (\text{mg l}^{-1}) = 1.44 \times \text{turbidity (NTU)} + 12.92, \quad n = 17, \quad r^2 = 0.93$$

$$\text{POM } (\text{mg l}^{-1}) = 0.18 \times \text{turbidity (NTU)} + 3.42, \quad n = 17, \quad r^2 = 0.94$$

$$\text{Chl-}a\ (\mu\text{g l}^{-1}) = 4.63 \times \text{fluorometry } (\%) + 1.65, \quad n = 16, \quad r^2 = 0.92$$

Food dilution and quality, herein estimated as percent organic content of SPM (POM:SPM ratio) and percent chl-*a* content of POM (chl-*a*:POM ratio), respectively, were calculated as follows:

$$\text{POM : SPM } (\%) = (\text{POM } (\text{mg l}^{-1})/\text{SPM } (\text{mg l}^{-1})) \times 100$$

$$\text{Chl-}a\text{ : POM } (\%) = (\text{chl-}a\ (\text{mg l}^{-1})/\text{POM } (\text{mg l}^{-1})) \times 100$$

2.6. Historical data of water temperature

Daily water temperatures (WT) in Bourgneuf Bay were calculated between January 1970 and December 2006, using the following regression (Haure and Baud, 1995):

$$\text{WT} = 0.8703 \times h + 0.036 \times \text{TC} - 0.0969$$

Daily atmospheric temperatures (AT) were obtained from Météo-France's Climathèque database (Noirmoutier station, 2°15′24″W, 47°00′18″N) and tidal coefficients (TC) using the Marées dans le monde 2.02© software.

2.7. Statistical analysis

Sigmastat 3.1 (Systat software) was used to check the normality and heteroscedasticity of data distributions and then to perform statistical analyses. Temporal and spatial variations of environmental factors were compared by Student t-tests or two-way parametric ANOVA, while correlation between them was determined by Spearman correlation tests. Analyses of data from histological determinations, as well as larval and post-larval cumulative densities, were first performed with two-way parametric ANOVA within each reproductive cycle, and *a posteriori* by Student–Newman–Keuls (SNK) tests.

3. Results

3.1. Environmental variations

3.1.1. Seston quantity and quality

Over the sampling period, SPM, POM and chl-*a* concentrations were always higher at the HT site compared to the IT site

(Fig. 2A–C – two-way ANOVA, $p < 0.01$). The monthly mean POM:SPM ratio, used to estimate potential food dilution, was lower at the HT site in 2005 and 2006 (Fig. 3A, *t*-test, $p < 0.01$). On the other hand, the monthly mean chl-*a*:POM ratio, used to estimate food quality, was higher at the HT site in 2005 (Fig. 3B, *t*-test, $p < 0.01$), while no significant difference between sites was reported in 2006 (Fig. 3B, *t*-test, $p = 0.98$).

3.1.2. Fine-scale variations of water temperature and salinity: 2005–2006

Monthly mean water temperatures, largely typical of a northern temperate nearshore ecosystem, were not significantly different between the sites in 2005 and 2006 (Fig. 2D, Student *t*-test, $p = 0.95$ and $p = 0.99$, respectively). However, the summer period was warmer in 2006 vs. 2005, especially in July, where the mean water temperature was 1.5 °C higher (Fig. 2D). The daily amplitude of water temperature was higher at the HT site (Table 1, two-way ANOVA, $p < 0.01$). Monthly mean salinity, ranging from 29.0 to 35.3, was not significantly different between the sites in 2005 and 2006 (Student *t*-test, $p = 0.93$ and $p = 0.10$, respectively).

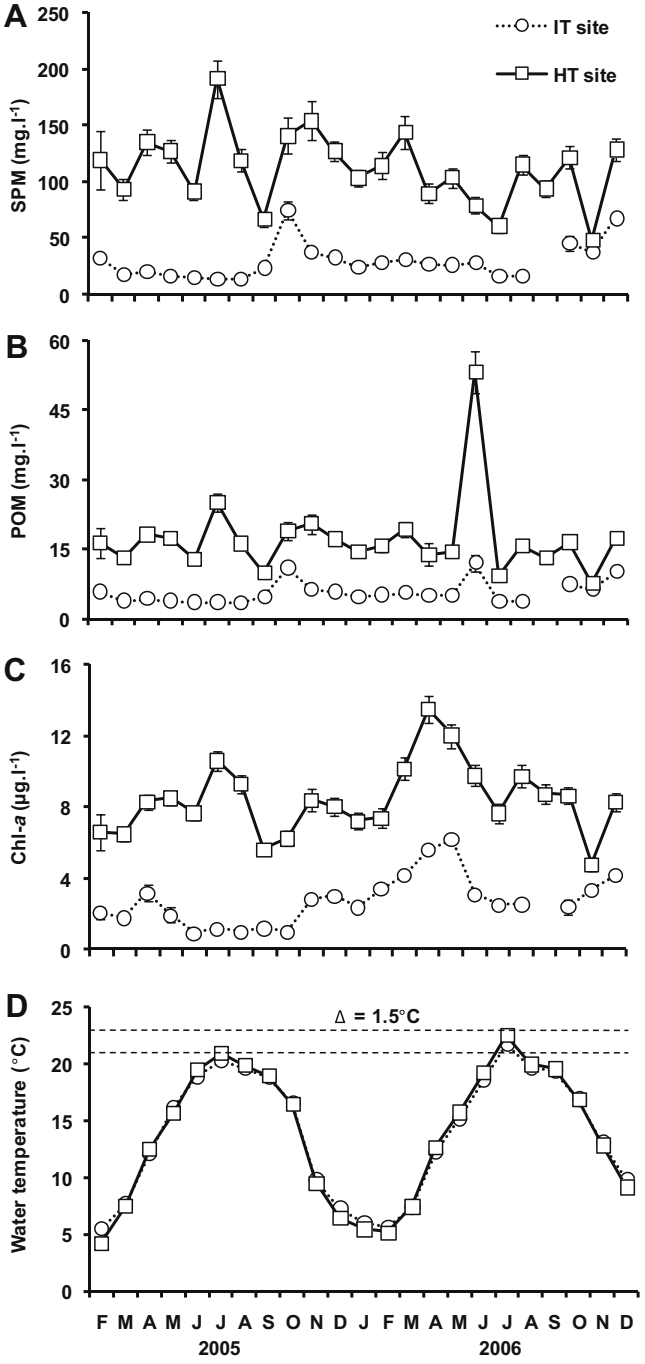

Fig. 2. Variations of suspended particulate matter (SPM, A), particulate organic matter (POM, B) and chlorophyll-*a* (chl-*a*, C) concentrations, and water temperature (D) at the northern high turbidity (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay, in 2005 and 2006. Means ± 95% confidence intervals.

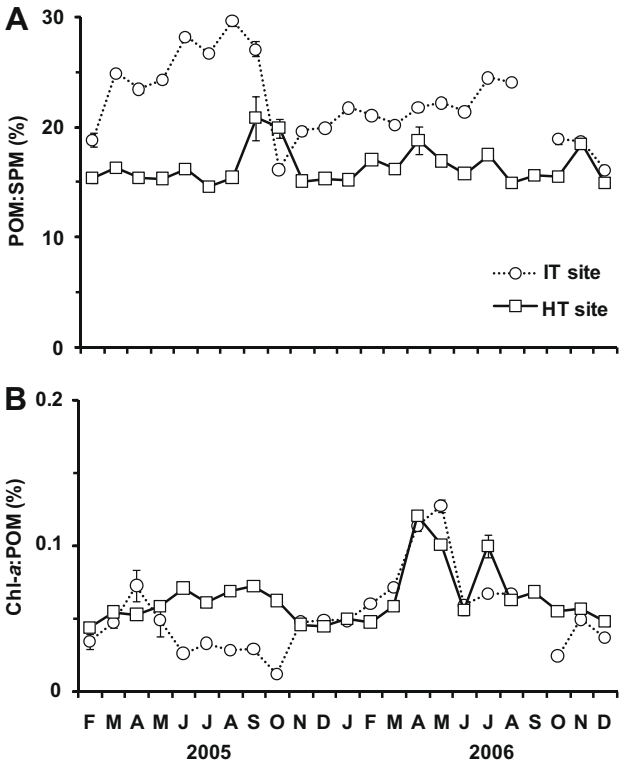

Fig. 3. Dilution (POM:SPM, A) and quality (chl-*a*:POM, B) of organic particles at northern high turbidity (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay in 2005 and 2006. Chl-*a*, chlorophyll-*a*; POM, particulate organic matter; SPM, suspended particulate matter. Means ± 95% confidence intervals.

Table 1
Mean daily amplitudes (±SD) of water temperature at the northern high turbidity (HT, La Coupelasse) and southern intermediate turbidity (IT, Gresseloup) sites of Bourgneuf Bay in 2005 and 2006.

	Year	*n* (days)	Amplitude of water temperature (°C)
HT site	2005	278	3.43 ± 2.01
	2006	349	2.23 ± 1.40
IT site	2005	251	2.39 ± 1.63
	2006	347	1.78 ± 1.29

3.1.3. Historical variations in water temperature

Historical annual mean and warmest-month calculated mean water temperatures are presented for Bourgneuf Bay from 1970 to 2006 (Fig. 4). For the 17-year period from 1970 to 1987, annual means were higher than the annual medians for only 2 years (11.8%), versus 15 years (83.3%) for the 18-year period from 1988 to 2006. This situation prevailed in 10 of 11 years (91%) from 1995 to 2006. Similarly, the warmest month means over the 17-year period from 1970 to 1987 were above the threshold temperature for successful reproduction (20 °C – Chávez-Villalba et al., 2002; Rico-Villa et al., 2008) only 2 years (11.8%), whereas over

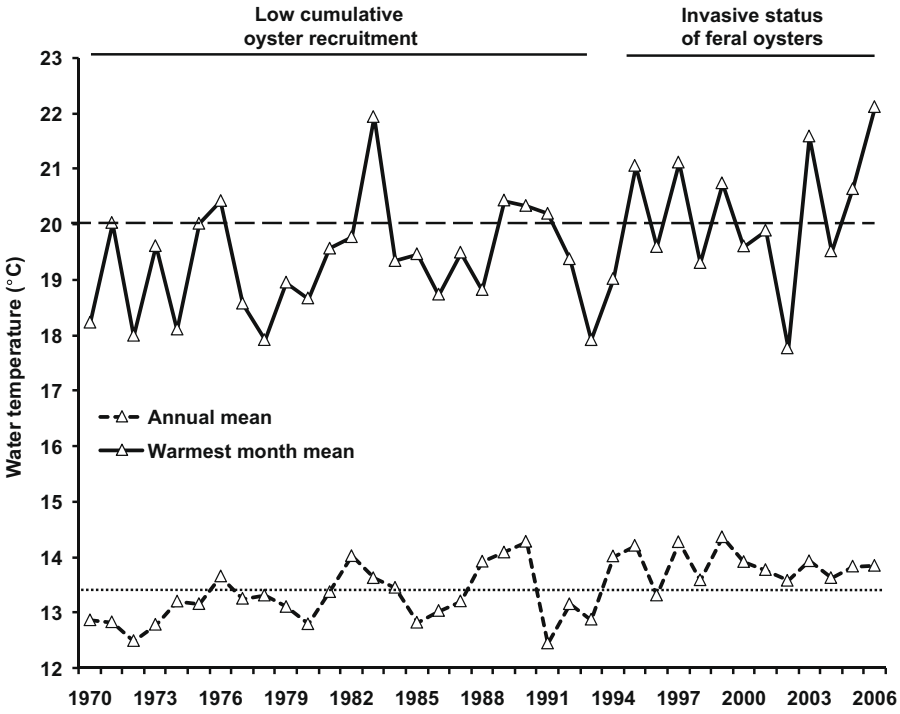

Fig. 4. Annual mean and warmest month mean of water temperature since the introduction of *Crassostrea gigas* in the 1970s (Météo-France, Climathèque database, Noirmoutier, 2007), and relationship with the natural recruitment of feral oysters in Bourgneuf Bay (Goulletquer, 1995; Cognie et al., 2004, 2006; Martin et al., 2004, 2005). Dotted line corresponds to the median temperature (13.4 °C) of annual mean water temperature, dashed line corresponds to the minimal threshold (20 °C) for optimal *C. gigas* larval development.

the 18-year period from 1988 to 2006, this situation prevailed in 9 years (50%).

3.2. Microscopic determinations and oocyte size

Variations in oocyte size allowed identification of two distinct seasonal reproductive cycles in 2005 and 2006 (Fig. 5). In 2005, no significant difference was observed for mean oocyte diameter in intra-site (two-way ANOVA, $p = 0.85$) and inter-site (two-way ANOVA, $p = 0.81$) comparisons. Similarly, in 2006, no significant difference was observed for mean oocyte diameter in intra-site (two-way ANOVA, $p = 0.84$) and inter-site (two-way ANOVA, $p = 0.94$) comparisons. In both years, the oocyte growth stage began in the same periods (end of March–beginning of April). However, the mature stage, corresponding to the dominance of ready-to-spawn post-vitellogenetic oocytes in the gonads, was reached more quickly in 2006 than in 2005 (two vs. three months). Gonads entered a degenerating stage (evidence of atresia in unspawned oocytes such as cell size increase and clearer cytoplasm – Dutertre et al., in press), more prematurely in 2006 than in 2005 (July vs. August, respectively).

3.3. D-larva and post-larval densities

Cumulative D-larva densities showed significant differences related to both year and site (Figs. 6 and 7, two-way ANOVA, $p < 0.05$ and $p < 0.01$, respectively). Cumulative D-larva densities were higher at the HT site for both years (SNK-tests, $p < 0.05$ for 2005 and $p < 0.01$ for 2006). For the IT site, cumulative D-larva densities were higher in 2006 compared to 2005 (SNK-test, $p < 0.05$), while, for the HT site, no significant differences were observed between the two years (SNK-test, $p = 0.30$). At both sites, D-larvae appeared at the same periods: over two months in 2005, from the beginning of July to the beginning of September, with a marked increase of

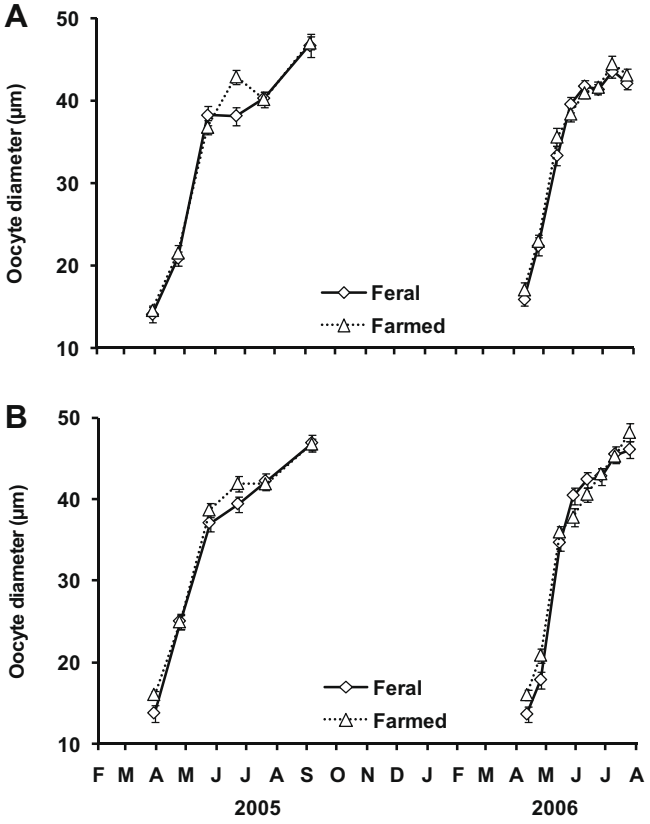

Fig. 5. Mean oocyte diameters (±95% IC) for feral and farmed oysters, *Crassostrea gigas*, at northern high turbidity (HT, A) and southern intermediate turbidity (IT, B) sites of Bourgneuf Bay in 2005 and 2006.

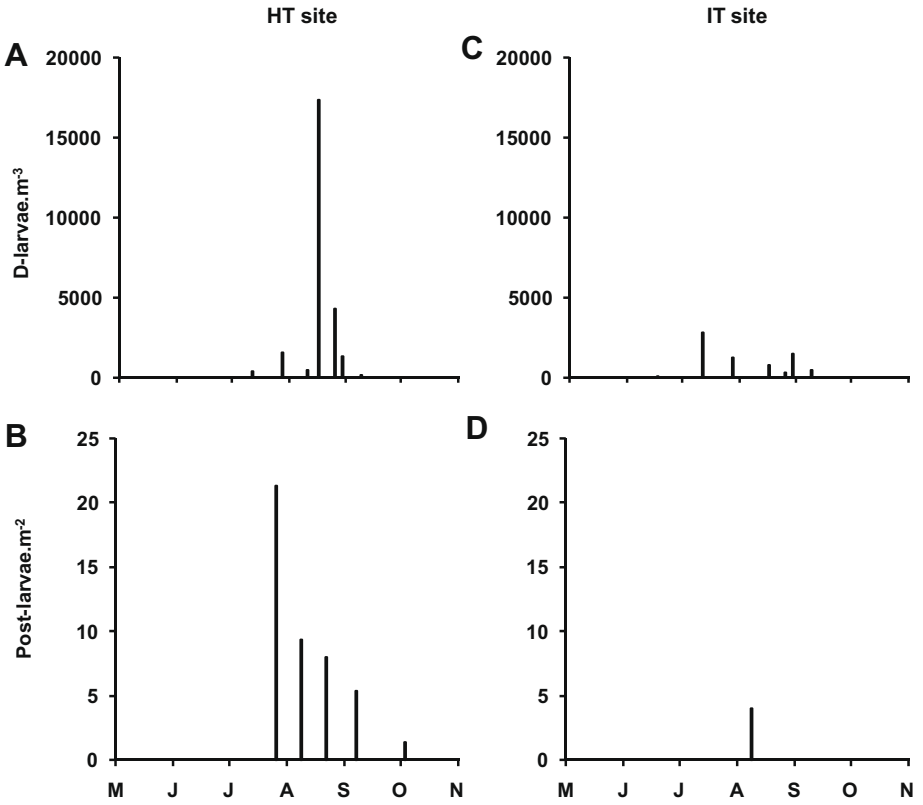

Fig. 6. D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year 2005.

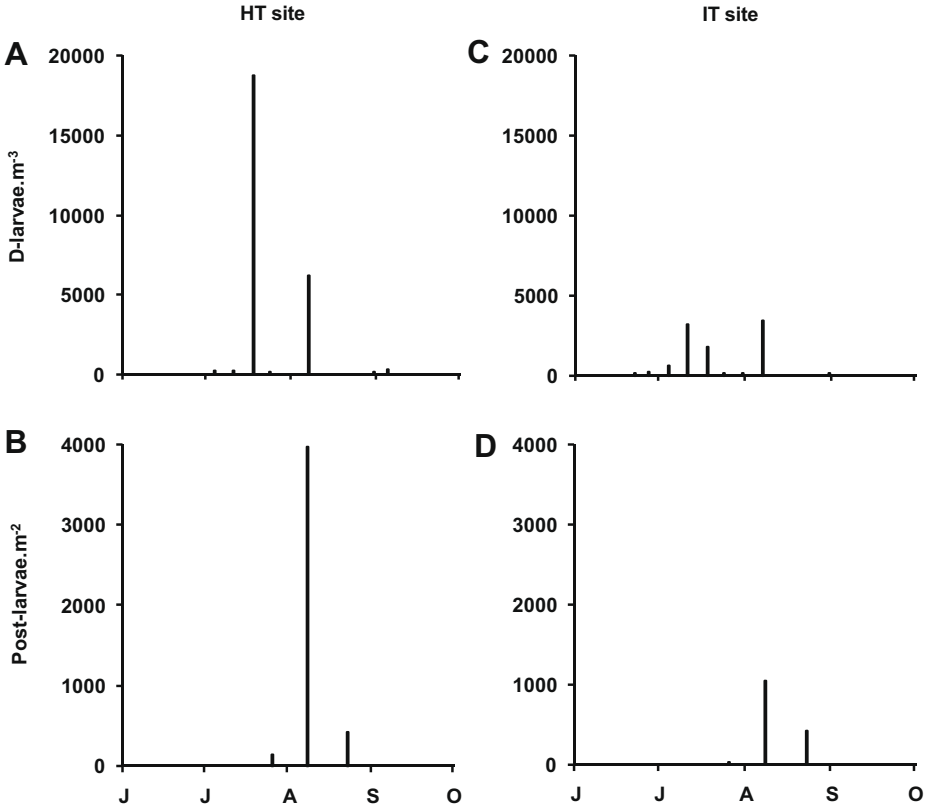

Fig. 7. D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year 2006.

the planktonic larva densities observed at the end of August at the HT site. In 2006, the HT site showed two main peaks of planktonic larva densities, at the end of July and at the beginning of August, while, at the same periods, two smaller peaks of D-larva densities were recorded at the IT site.

Cumulative natural post-larval recruitment also showed significant differences related to both year and site (Figs. 6 and 7, two-way ANOVA, $p < 0.01$). Natural recruitment was much higher in 2006 compared to 2005 at both sites (SNK-tests, $p < 0.001$ for the HT site and $p < 0.05$ for the IT site). Inter-site differences in the monthly post-larval counts were also evident, with proportionately higher counts at the HT site in both 2005 and 2006.

4. Discussion

4.1. Water temperature and recent oyster invasion

At approximately 28 000 tons, the feral oyster stock in Bourgneuf Bay equals 70% of the annual farmed oyster production (Cognie et al., 2004; Martin et al., 2004, 2005). Water temperature variations, since the introduction of *C. gigas* for aquaculture, clearly show that the onset of the feral oyster invasion coincided with a marked water warming (Fig. 4). Indeed, between 1970 and 1995, when annual mean water temperature was usually lower than the median temperature (13.4 °C), cumulative feral oyster recruitment was very low (Le Borgne et al., 1973; Gruet et al., 1976; Goulletquer, 1995). Massive recruitment of feral oysters, observed since 1995 (Cognie et al., 2006) corresponded to the beginning of the period where summer months often showed water temperature higher than 20 °C, which is required for successful *C. gigas* larval development in hatcheries (Arakawa, 1990; Shatkin et al., 1997; Chávez-Villalba et al., 2002; Rico-Villa et al., 2008). These quantitative historical data thus support earlier hypotheses of a relationship between *C. gigas* proliferation in cool temperate European ecosystems and global warming (Diederich et al., 2005; Ruesink et al., 2005; Smaal et al., 2005). Among the temperature-related variables which could contribute to this proliferation are those which chiefly affect larval survival and subsequent recruitment of feral oysters: oocyte reserves, spawning period and seston conditions (Baldwin and Newell, 1995; Powell et al., 2002; Chávez-Villalba et al., 2003; Rico-Villa et al., 2008).

4.2. Oocyte fate timed by water temperature thresholds

During two successive reproductive cycles of *C. gigas*, oocyte diameter variations showed that the field reproductive cycle was timed by discrete water temperature thresholds (Dutertre et al., in press). The oocyte growing stage, characterized by both an increase in size and in vittelin reserves (see Gosling (2003) for recent review), began when spring water temperature reached 8–10 °C. The mature stage was reached more quickly in 2006 than in 2005 (two vs. three months), corresponding to a reduced daily amplitude of water temperatures in 2006, and also to a greater energy level of breeders due to higher spring food quality (chl-*a*:POM ratio) and/or recovery of energy from the large amount of reabsorbed atretic oocytes at the end of summer 2005 (Dutertre et al., in press). Although early partial spawns could be detected when daily variations in water temperature briefly exceeded 18 °C, water temperatures of 15–18 °C cause mature, unspawned oocytes to enter atresia (Dutertre et al., in press). Major spawning activities were recorded when summer water temperature, higher than 20 °C, could efficiently sustain *C. gigas* larval development (Chávez-Villalba et al., 2002; Rico-Villa et al., 2008).

Similar oocyte size in farmed and feral oysters at both sites indicated that future fertilized eggs would contain equivalent amounts of vitellus for the endotrophic and mixotrophic larval stages (Lucas et al., 1986; His and Seaman, 1992; Cannuel and Beninger, 2005). This result is in agreement with the observation that variations in reproductive effort in *C. gigas* reflect variations in gamete quantity rather than quality (Caers et al., 2002; Chávez-Villalba et al., 2003; Cannuel and Beninger, 2005).

4.3. Planktonic larval life

Maximal planktonic larva densities in the water column were observed during defined summer periods in which high oyster fecundity was synchronized with a water temperature higher than 20–22 °C. D-larva densities corresponded to the patterns of breeder spawning strategy at both sites in 2005 and 2006, but early spawns, which occurred when water temperature was below the threshold allowing an optimal larval development (Dutertre et al., in press), were not accompanied by larval presence. Moreover, although IT oysters had more pronounced spawns compared to HT oysters in both years (Dutertre et al., in press), D-larva densities were higher at the HT site, which presented slightly, but non-statistically significant, higher summer temperatures. This may also be due to the significantly higher level of chlorophyll-*a* at the HT site; in other words, the poor food quality at the HT site was amply compensated by the sheer amount of food available for the larvae.

4.4. Feral oyster recruitment

Natural post-larval recruitment at both HT and IT sites was much higher in 2006 (4540 and 1489 annual settled post-larvae m^{-2}, respectively) compared to 2005 (45 and 4 annual settled post-larvae m^{-2}, respectively). Although 2006 could be considered an exceptionally favorable year for oyster reproduction and post-larval recruitment in relation to the warmer summer temperatures, natural recruitment in Bourgneuf Bay remained very low compared to more southern coastal ecosystems. Indeed, the best natural recruitments in Arcachon Bay over the past 20 years were reported in 2003 and 2006 with more than 60 000 settled post-larvae m^{-2} of limed tiles (Auby et al., 2006). Environmental conditions at the HT site, notably the chlorophyll-*a* levels, regardless of the organic matter dilution, appear to promote local feral oyster recruitment. This is confirmed by oyster-farmer practices over the past several years, which preferentially use the HT site to install artificial spat collectors (Marion Petit, Section Régionale Conchylicole, Bouin, France, personal communication). Once established, large feral oyster reefs can disrupt flow, limit larval dispersal, and offer substrate for settlement, enhancing local post-larval recruitment at the HT site.

5. Conclusion

The historical data presented here clearly show that *C. gigas* proliferation in the Bourgneuf Bay ecosystem corresponds to warmer water temperatures, particularly since 1995. A similar evolution in water temperatures has been recorded at more northerly sites (Wadden Sea), also corresponding to increasing *C. gigas* recruitment (Diederich et al., 2005). The underlying processes of reproduction and development are acutely sensitive to such warming through the threshold temperatures of oocyte growth and larval development, and ultimately greater recruitment of post-larval feral oysters, as shown by the recent fine-scale temporal data of the present study. A continuation of the warming trend in water temperatures should thus produce an intensification of this proliferation, and a range extension northward in shallow European bays, including those used for oyster farming. Given the now

near-ubiquitous distribution of *C. gigas* in temperate coastal habitats, these observations should serve to alert the marine environment research community to potentially similar situations worldwide.

Acknowledgements

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