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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.

Keywords: Aquaculture; Climate warming; Coastal waters; *Crassostrea gigas*; Reproductive cycle; Oyster larvae; Settlement; Turbidity

1. Introduction

Suspension-feeding bivalves are coastal ecosystem engineers that regulate matter and energy fluxes by coupling pelagic and benthic processes (see Dame and

43 Olenin, 2005 for reviews). In the twentieth century, over-exploitation, pollution, and
44 disease led to a worldwide decline in native oyster populations, accompanied by
45 economic losses and ecological changes (Newell, 1988; Quayle, 1988; Ruesink et
46 al., 2005). The Pacific cupped oyster, *Crassostrea gigas*, was voluntarily introduced
47 in several new coastal areas around the world for aquaculture purposes, because of
48 its rapid growth rate, high tolerance to environmental variations and low susceptibility
49 to oyster diseases (Coleman, 1986; Smith et al., 1986; Grizel and Héral, 1991).

50 Although successful introductions of *C. gigas* occurred particularly in northern
51 temperate countries of Europe and North America, water temperatures precluded
52 substantial larval recruitment in the northernmost regions (Le Borgne et al., 1973;
53 Gruet et al., 1976; Goulletquer, 1995; Drinkwaard, 1999). France is a particularly
54 interesting case, since the occurrence of massive and regular feral *C. gigas*
55 recruitments in the southern Atlantic regions, but not in the northern ones, suggested
56 that the limit for the successful larval development was situated south of Bourgneuf
57 Bay (Goulletquer and Héral, 1991; Robert and Gérard, 1999). However, in the past
58 decade, feral oysters have proliferated on northern European Atlantic coasts,
59 unrelated to new introductions, and *C. gigas* is now considered to be an invasive
60 organism from Spain to the North Sea (Reise et al., 1999; Wehrmann et al., 2000;
61 Cognie et al., 2006; Brandt et al., 2008). This phenomenon is particularly visible in
62 northern French turbid bays, where the feral *C. gigas* build long-lasting reefs and
63 colonize racks on which are attached farmed *C. gigas* bags (Martin et al., 2004;
64 2005). In these areas, trophic competition with feral oysters has been suggested to
65 explain the decline in farmed oyster growth performance in the last ten years (Cognie
66 et al., 2006). Although reproduction performances of farmed adult oysters are being

67 elucidated (Dutertre et al., in revision), field studies on natural recruitment are also
68 necessary to understand the recent feral oyster invasion (Underwood and
69 Fairweather, 1989; Grosberg and Levitan, 1992; Smaal et al., 2005).

70 Optimal larval development of *C. gigas* requires a water temperature higher
71 than 22℃ during at least two weeks (Arakawa, 1990; Shatkin et al., 1997; Rico-Villa
72 et al., 2008) and oyster larvae are affected by food quality and quantity (Baldwin and
73 Newell, 1995; Powell et al., 2002; Rico-Villa et al., 2008). As larval survival is the
74 determining element for the settlement of feral oyster populations (Gosling, 2003),
75 environmental influences on larval development need to be clarified by field studies,
76 especially in turbid coastal waters which are characterized by seasonal and short-
77 term variations of the environmental conditions (Mann, 1982).

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

83

84 **2. Materials and methods**

85 **2.1. Adult oyster sampling and tissue fixation**

86 Feral and farmed oysters were collected at two oyster-farming sites in
87 Bourgneuf Bay, between February 2005 and July 2006 (Fig. 1, Haure and Baud,
88 1995). The northern site, La Coupelasse (47°1’ 34.7’’N, 2°1’ 55.9’’W) , is a high -

89 turbidity mudflat compared to the southern sandy-muddy bottom site, Gresseloup
90 (46°57’ 2.6’’N, 2°7’ 53.4’’W) .

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

103

104 **2.2. Histological preparation**

105 After fixation, a 0.5 mm-thick slice of the visceral mass was removed from the
106 region along the line connecting the left and right palp-gill junctions (Morales-Alamo
107 and Mann, 1989). The tissue was rinsed under running water overnight to eliminate
108 excess Bouin’s solution, dehydrated and prepared for paraffin embedding.
109 Embedded tissues were sliced with a microtome to obtain 10 histological sections per
110 individual, 7 µm in thickness. These sections were rehydrated, stained with modified
111 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℃ for at least one week.

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 per oyster). Oocyte diameter was then calculated as follows:

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

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 to 12.0 µm), growing (12.1 to 30.0 µm), mature (30.1 to 41.0 µm) or atretic (41.1 to 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 to 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,

157 NTU) and chlorophyll-*a* (chl-*a*) concentration (fluorometry, %) every hour. The
158 corresponding monthly means were plotted with their 95 % confidence intervals (n =
159 720).

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

163 Quantity

164 Suspended Particulate Matter – the total amount of particles, quality not specified

165 Particulate Organic Matter (POM) – potentially digestible particles, but quality not
166 specified

167 Chlorophyll-*a* – amount of available phytoplankton, proportion of the available
168 particulate matter not specified

169 Quality

170 POM:SPM – an indication of the organic content of the SPM (dilution of POM)

171 Chl-*a*:POM – an indication of the quality of the organic matter

172 In order to characterize potential food amount, availability, and quality, field
173 calibrations for suspended matter were performed simultaneously from both probe
174 records and natural seawater samples collected at each oyster sampling site over
175 two tidal cycles. Some seawater samples (n = 17) were dried at 60℃ for 48 h and
176 then ashed at 450℃ for 4 h (Barillé-Boyer et al., 2003) to obtain SPM and POM
177 concentrations ($mg.l^{-1}$) respectively, while other samples (n = 16) were analyzed by
178 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:

SPM (mg.l^{-1}) = 1.44 × turbidity (NTU) + 12.92, n = 17, r^2 = 0.93

POM (mg.l^{-1}) = 0.18 × turbidity (NTU) + 3.42, n = 17, r^2 = 0.94

Chl-*a* (µg.l^{-1}) = 4.63 × fluorometry (%) + 1.65, n = 16, 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:

POM:SPM (%) = (POM (mg.l^{-1}) / SPM (mg.l^{-1})) × 100

Chl-*a*:POM (%) = (chl-*a* (mg.l^{-1}) / POM (mg.l^{-1})) × 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):

$WT = 0.8703 \times AT + 0.036 \times TC - 0.0969$

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, B and 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

221 Monthly mean water temperatures, largely typical of a northern temperate
222 nearshore ecosystem, were not significantly different between the sites in 2005 and
223 2006 (Fig. 2D, Student t-test, $p = 0.95$ and $p = 0.99$, respectively). However, the
224 summer period was warmer in 2006 vs. 2005, especially in July, where the mean
225 water temperature was 1.5℃ higher (Fig. 2D). The d aily amplitude of water
226 temperature was higher at the HT site (Table 1, two-way ANOVA, $p < 0.01$). Monthly
227 mean salinity, ranging from 29.0 to 35.3, was not significantly different between the
228 sites in 2005 and 2006 (Student t-test, $p = 0.93$ and $p = 0.10$, respectively).
229
230 *3.1.3 Historical variations in water temperature*

231 Historical annual mean and warmest-month calculated mean water
232 temperatures are presented for Bourgneuf Bay from 1970 – 2006 (Fig. 4). For the 17-
233 year period from 1970 – 1987, annual means were higher than the annual medians
234 for only 2 years (11.8%), versus 15 years (83.3%) for the 18-year period from 1988 –
235 2006. This situation prevailed in 10 of 11 years (91%) from 1995 – 2006. Similarly,
236 the warmest month means over the 17-year period from 1970 – 1987 were above the
237 threshold temperature for successful reproduction (20℃ – Chávez-Villalba et al.,
238 2002; Rico-Villa et al., 2008) only 2 years (11.8%), whereas over the 18-year period
239 from 1988 – 2006, this situation prevailed in 9 years (50%).
240
241 **3.2. Microscopic determinations and oocyte size**

242 Variations in oocyte size allowed identification of two distinct seasonal
243 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 revision), 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 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 28000 t, 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℃), 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℃, 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 revision). 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℃. 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 revision). Although early partial spawns could be detected when daily variations in water temperature briefly exceeded 18℃, water temperatures of 15 – 18℃ cause mature, unspa wned oocytes to enter atresia (Dutertre et al. in revision). Major spawning activities were recorded when summer water temperature, higher than 20℃, could efficien tly 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℃. D-larva de nsities 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 revision), 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 revision), 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

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

351

352 **5. Conclusion**

353 The historical data presented here clearly show that *C. gigas* proliferation in
354 the Bourgneuf Bay ecosystem corresponds to warmer water temperatures,
355 particularly since 1995. A similar evolution in water temperatures has been recorded
356 at more northerly sites (Wadden Sea), also corresponding to increasing *C. gigas*
357 recruitment (Diederich et al, 2005). The underlying processes of reproduction and
358 development are acutely sensitive to such warming through the threshold
359 temperatures of oocyte growth and larval development, and ultimately greater
360 recruitment of post-larval feral oysters, as shown by the recent fine-scale temporal
361 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.

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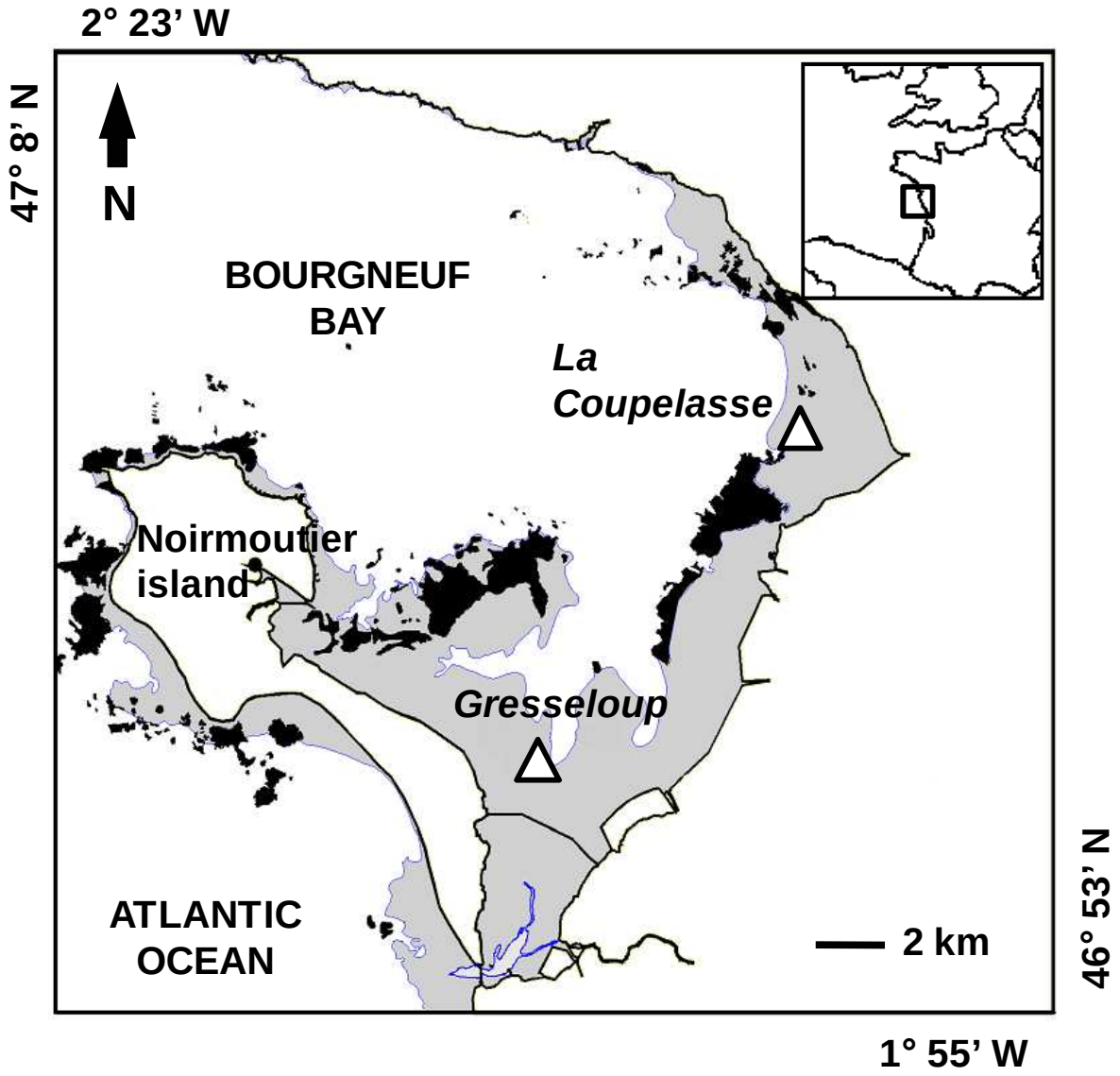
533 Table 1. Mean daily amplitudes (± SD) of water temperature at the northern high
534 turbidity (HT, La Coupelasse) and southern intermediate turbidity (IT, Gresseloup)
535 sites of Bourgneuf Bay in 2005 and 2006.

	Year	n (days)	Amplitude of water temperature (℃)
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

536

537

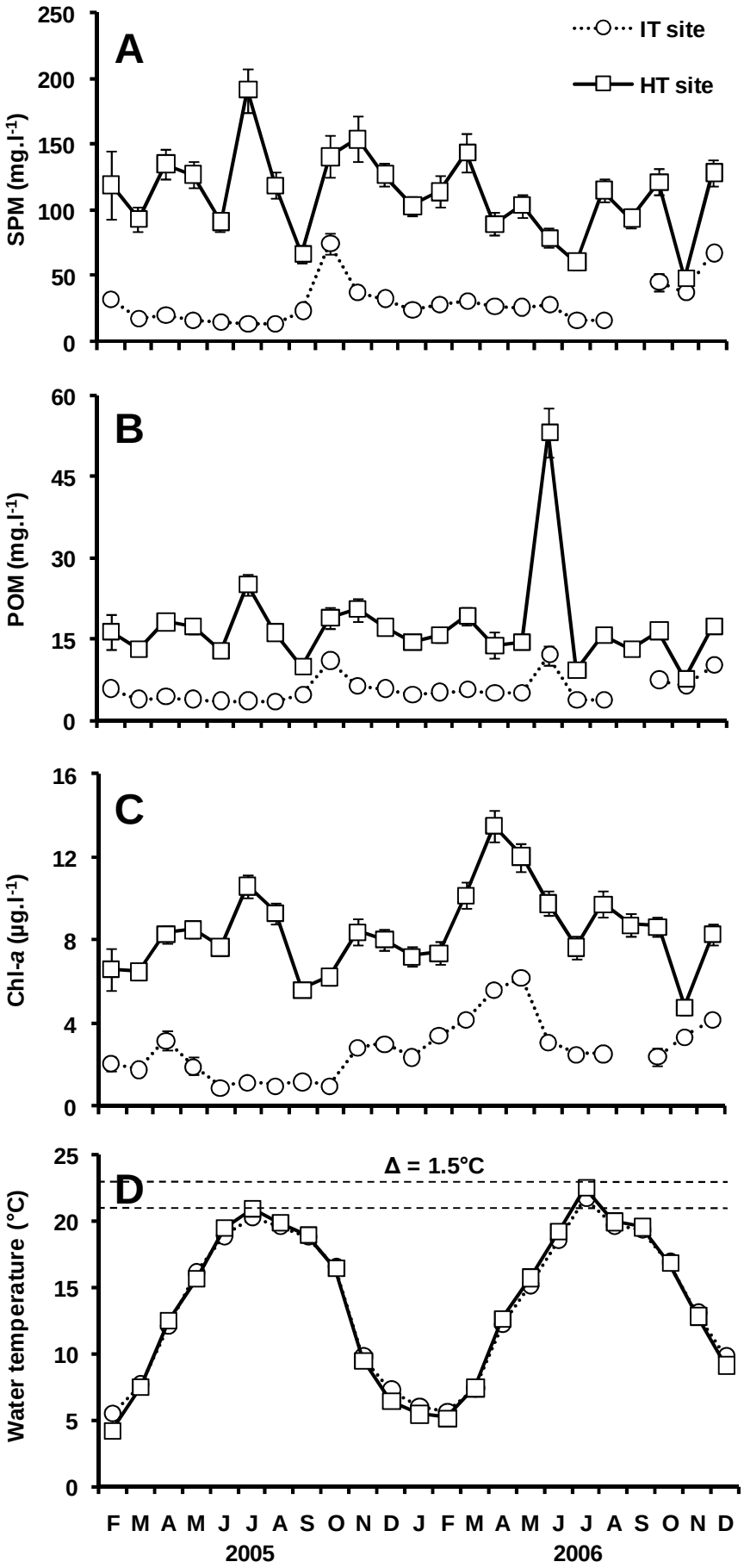


538

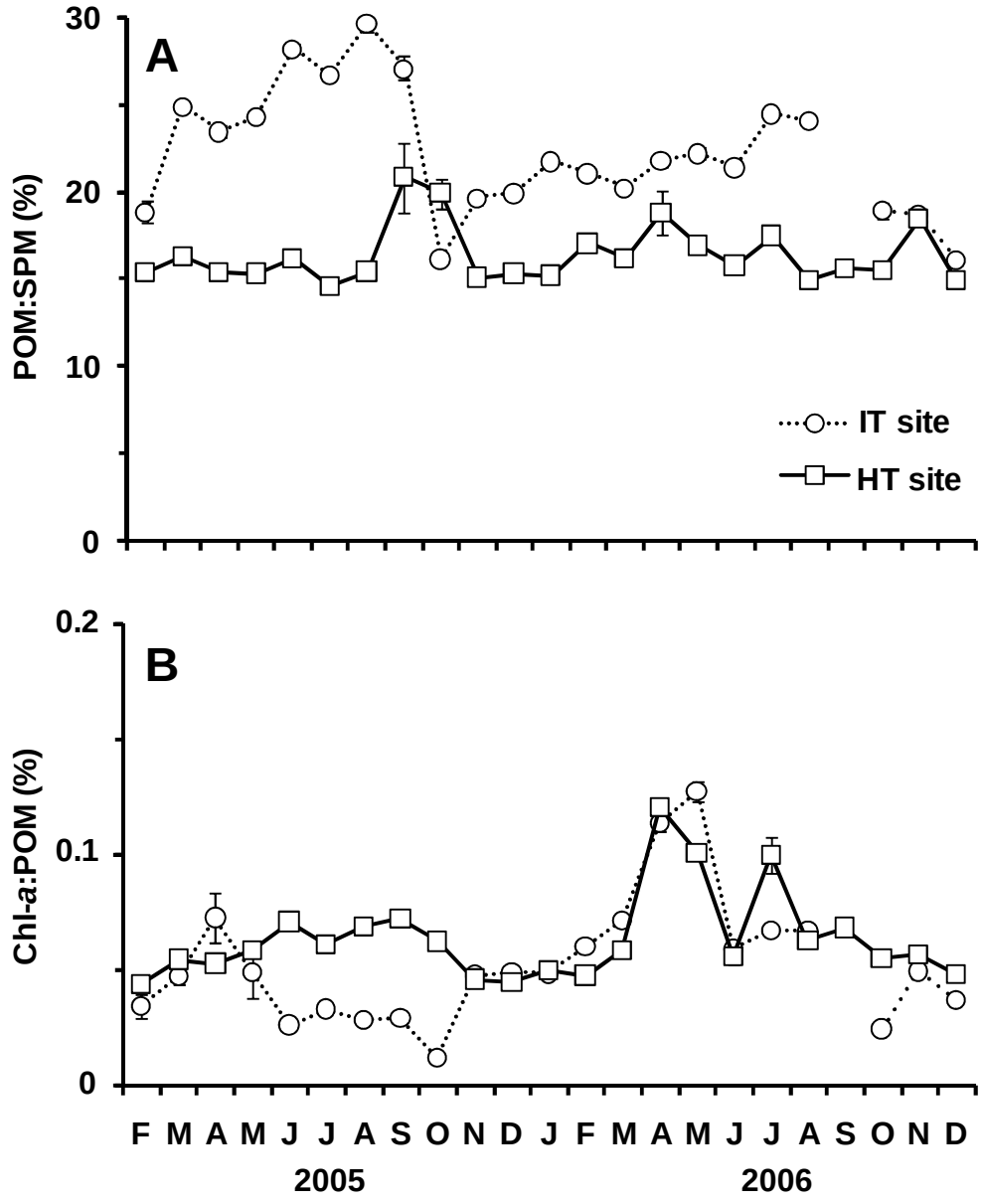
539 **Fig. 1**. Location of northern (La Coupelasse) and southern (Gresseloup) oyster

540 sampling sites (**Δ**) in Bourgneuf Bay. The intertidal zone and rocks are represented

541 by gray and black areas respectively (modified from Barillé et al., 2000).

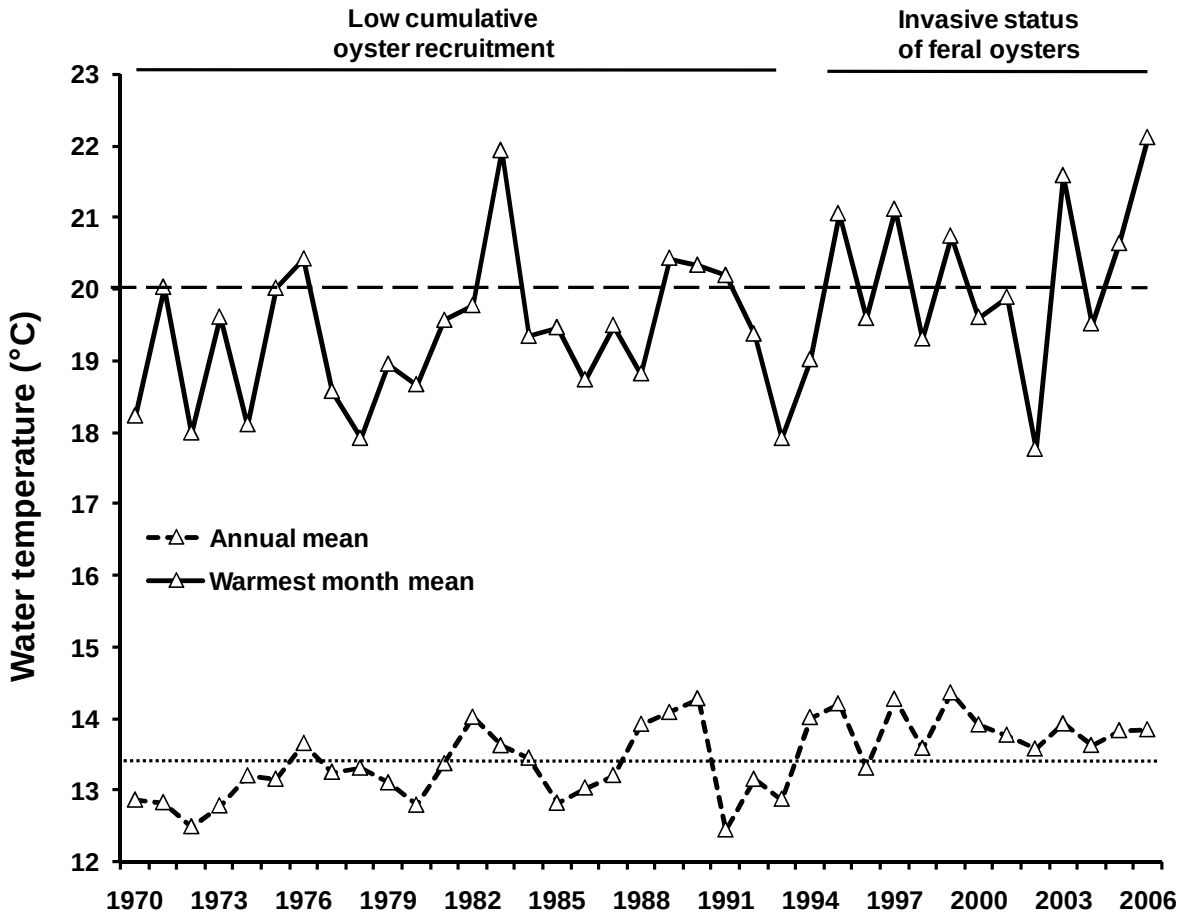

A
IT site
HT site
SPM (mg.l-1)
250
200
150
100
50
0
B
POM (mg.l-1)
60
45
30
15
0
C
Chl-a (µg.l-1)
16
12
8
4
0
D
Δ = 1.5°C
Water temperature (°C)
25
20
15
10
5
0
F M A M J J A S O N D J F M A M J J A S O N D
2005
2006

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



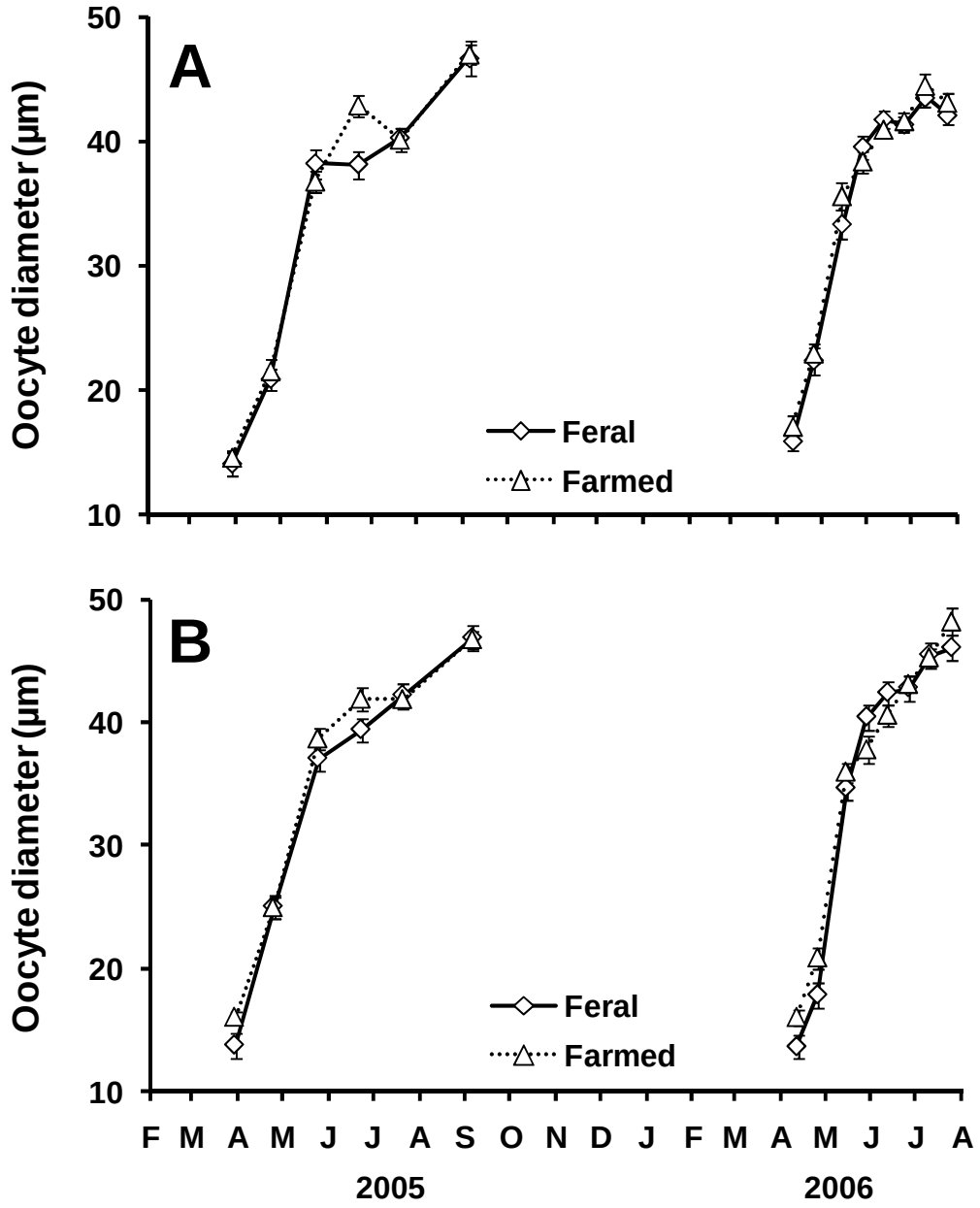
547

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



552

553 **Fig. 4**. Annual mean and warmest month mean of water temperature since the
554 introduction of *Crassostrea gigas* in the 1970's (Météo-France, Climathèque
555 database, Noirmoutier, 2007), and relationship with the natural recruitment of feral
556 oysters in Bourgneuf Bay (Goulletquer, 1995; Cognie et al., 2004; 2006; Martin et al.,
557 2004; 2005). Dotted line corresponds to the median temperature (13.4℃) of annual
558 mean water temperature, dashed line corresponds to the minimal threshold (20℃)
559 for optimal *C. gigas* larval development.

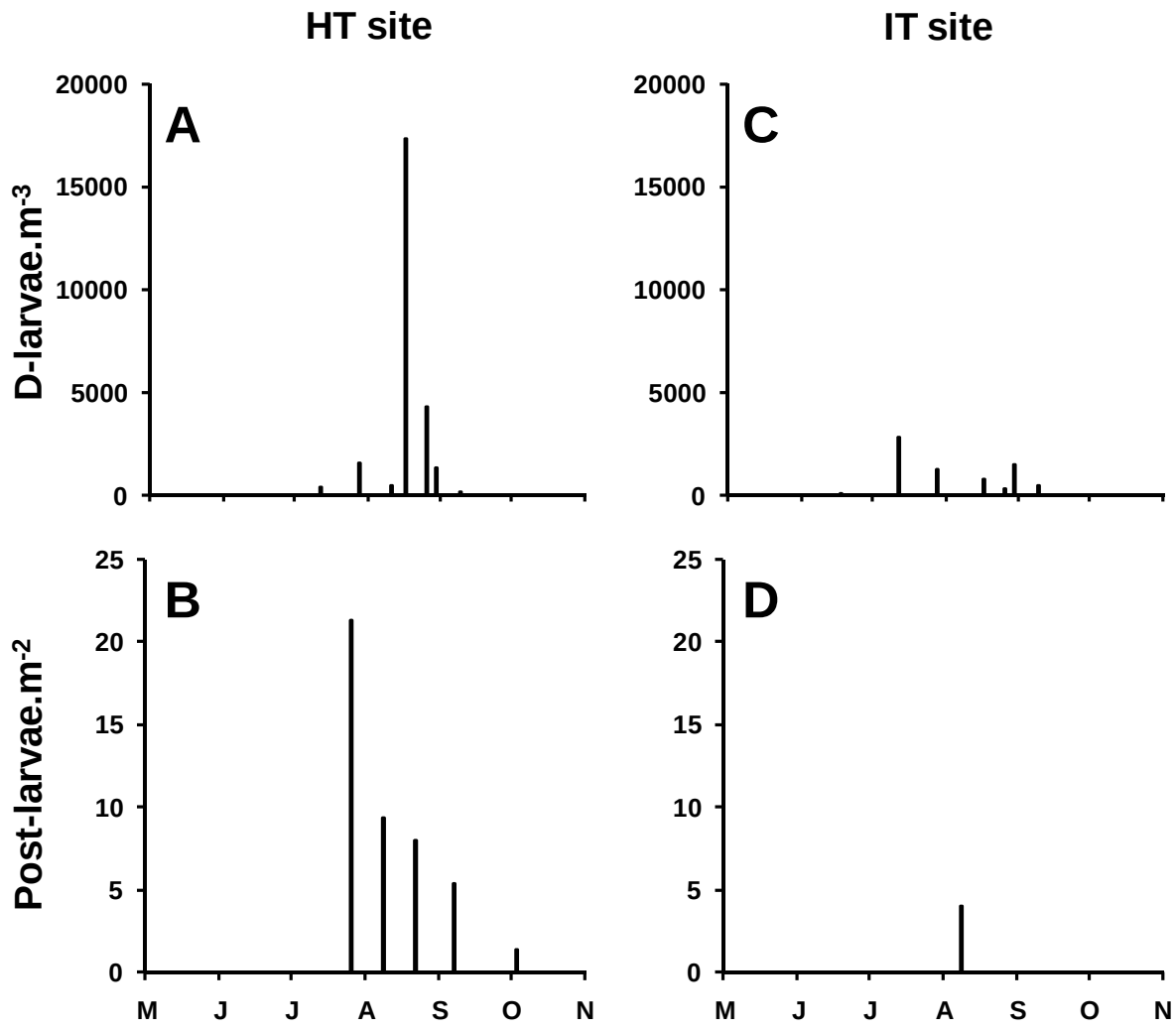


560

561 **Fig. 5**. Mean oocyte diameters (± 95% IC) for feral and farmed oysters, *Crassostrea*

562 *gigas*, at northern high turbidity (HT, A) and southern intermediate turbidity (IT, B)

563 sites of Bourgneuf Bay in 2005 and 2006.

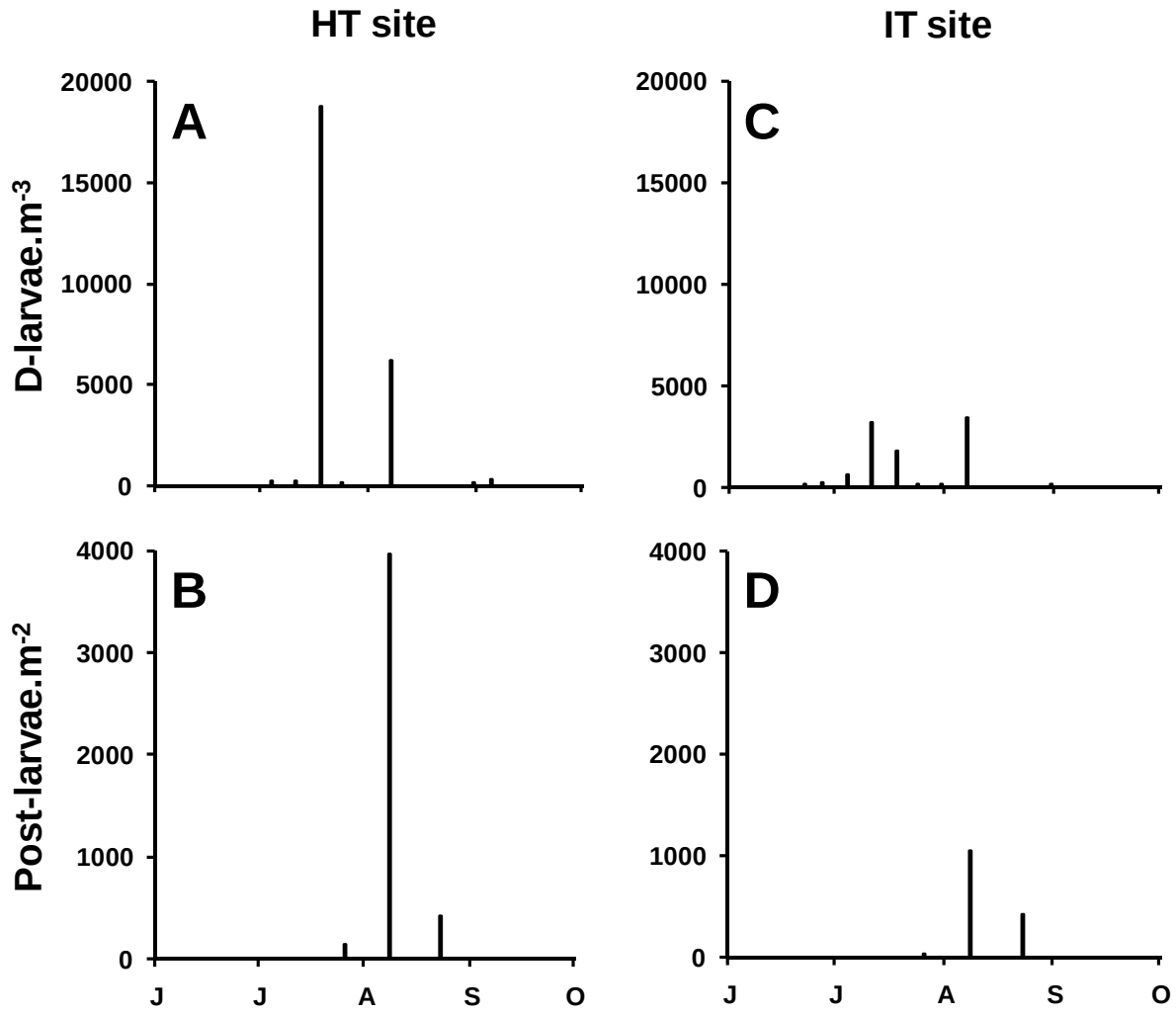


564

565 **Fig. 6**. D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity

566 (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year

567 2005.



568

569 **Fig. 7**. D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity

570 (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year

571 2006.

572