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2

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

5

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20 Abstract

1
2
3 21 The recent appearance and invasion of feral oysters (*Crassostrea gigas*) along
4
5 22 the northern European Atlantic coast, underscores the necessity to investigate the
6
7
8 23 relationship between environmental variables, reproductive physiology, larval
9
10 24 development and recruitment. We studied these relationships at both high (HT) and
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12
13 25 intermediate (IT) – turbidity sites, through historical data on water temperatures,
14
15 26 multi-parameter environmental probes, histological analyses, and field collections of
16
17
18 27 planktonic larvae and settled post-larvae in 2005 and 2006. A progressive warming
19
20 28 trend was observed, especially since 1995, when oyster proliferation first became
21
22
23 29 severe. Threshold temperatures for oocyte growth, larval development and
24
25 30 settlement were achieved in both 2005 and 2006. The HT site showed greater
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27
28 31 numbers of larvae and post-larvae than the IT site for both years, with the highest
29
30 32 numbers of post-larvae observed at both sites during the warmer summer of 2006.
31
32 33 These results suggest that increased temperatures in northern European waters allow
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34
35 34 successful reproduction, larval development, and recruitment of *C. gigas*. High
36
37 35 turbidity conditions further enhance this success.
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41 36

42 37 Keywords: Aquaculture, Climate warming, Coastal waters, *Crassostrea gigas*,
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45 38 Reproductive cycle, Oyster larvae, Settlement, Turbidity
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52 40 1. Introduction

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55 41 Suspension-feeding bivalves are coastal ecosystem engineers that regulate
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58 42 matter and energy fluxes by coupling pelagic and benthic processes (see Dame and
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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; Gouletquer, 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 (Gouletquer 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°C 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.

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 spat,) 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).

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

112 mounting medium (Beninger et al., 2001). Mounted histological sections were then
113 dried at 60°C for at least one week.

114

115 **2.3. Microscopic determinations and oocyte size measurements**

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

$$127 \text{ Oocyte diameter } (\mu\text{m}) = 2 \times \sqrt{(\text{oocyte area } (\mu\text{m}^2) / \pi)}$$

128 Monthly means (\pm 95 % confidence intervals, CI) of oocyte diameters were
129 calculated and used to determine the gonadal development stage (Lango-Reynoso et
130 al., 2000): early gametogenesis (3.0 to 12.0 μm), growing (12.1 to 30.0 μm), mature
131 (30.1 to 41.0 μm) or atretic (41.1 to 60 μm).

132 **2.4. Determinations of D-larva and post-larval densities**

134 Unambiguous identification of *C. gigas* larvae was achieved through a
1 preliminary inventory of larval bivalve species at the two study sites, followed by
2 135 preliminary inventory of larval bivalve species at the two study sites, followed by
3
4 136 identification using literature data (Rees, 1950; Le Pennec, 1978; His, 1991) and
5
6
7 137 computer image analysis of key shell characteristics (Lucia G 4.80 software).
8

9 138 During known oyster spawning periods, plankton samples were collected at the
10
11
12 139 northern and southern sites using a boat-mounted pump provided with a flowmeter.
13
14 140 Each plankton sample (1.5 m³) was fixed in 10% formaldehyde – seawater solution
15
16
17 141 and prepared for analysis as in Auby et al. (2002). Each sample was manually
18
19 142 homogenized with a loop-ended glass stick to avoid damage to larvae, and two 0.5
20
21
22 143 ml aliquots were transferred to Sedgewick-Rafter counting cells and observed using
23
24 144 a light microscope (Olympus AX70) in order to determine D-larva densities (shell
25
26
27 145 height = 57 to 105 µm; Rees, 1950; Le Pennec, 1978; His, 1991).
28

29
30 146 At each site, clusters of 10 striated tubular collectors (commonly used as
31
32 147 substrata for oyster spat settlement in the field; length = 120 cm, diameter = 2 cm)
33
34
35 148 were tied side by side to oyster racks (3.0 × 1.0 m) at 0.6 m from the bottom. The
36
37 149 clusters were rolled up at the end of each tidal cycle to count the post-larval (i.e.
38
39
40 150 recently-settled spats) density, and replaced with new clusters for the next tidal cycle.
41

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44 45 46 152 **2.5. Environmental monitoring**

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49 153 Multi-parameter water quality probes (YSI 6600) were fixed to oyster racks
50
51
52 154 installed at each sampling site, to record temperature (°C), salinity (from
53
54
55 155 conductivity), suspended particulate matter (SPM) concentration (nephelometry,
56
57 156 NTU) and chlorophyll-*a* (chl-*a*) concentration (fluorometry, %) every hour. The
58
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157 corresponding monthly means were plotted with their 95 % confidence intervals (n =
158 720).

159 Food is implicitly defined as ingestible matter. Since we do not know what,
160 precisely, the oysters are ingesting, we can only use indicators of available food.

161 These must take into account:

162 Quantity

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

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

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

168 Quality

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

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

171 In order to characterize potential food amount, availability, and quality, field
172 calibrations for suspended matter were performed simultaneously from both probe
173 records and natural seawater samples collected at each oyster sampling site over
174 two tidal cycles. Some seawater samples (n = 17) were dried at 60°C for 48 h and
175 then ashed at 450°C for 4 h (Barillé-Boyer et al., 2003) to obtain SPM and POM
176 concentrations (mg.l⁻¹) respectively, while other samples (n = 16) were analyzed by
177 spectrophotometry after extraction with acetone (Lorenzen, 1967) to determine chl-*a*

188 concentrations ($\mu\text{g.l}^{-1}$). Linear regressions obtained from field samples were used to
 189 transform hourly probe records into concentrations as follows:

$$190 \text{ SPM (mg.l}^{-1}\text{)} = 1.44 \times \text{turbidity (NTU)} + 12.92, n = 17, r^2 = 0.93$$

$$191 \text{ POM (mg.l}^{-1}\text{)} = 0.18 \times \text{turbidity (NTU)} + 3.42, n = 17, r^2 = 0.94$$

$$192 \text{ Chl-a (}\mu\text{g.l}^{-1}\text{)} = 4.63 \times \text{fluorometry (\%)} + 1.65, n = 16, r^2 = 0.92$$

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

$$196 \text{ POM:SPM (\%)} = (\text{POM (mg.l}^{-1}\text{)} / \text{SPM (mg.l}^{-1}\text{)}) \times 100$$

$$197 \text{ Chl-a:POM (\%)} = (\text{chl-a (mg.l}^{-1}\text{)} / \text{POM (mg.l}^{-1}\text{)}) \times 100$$

198 2.6. Historical data of water temperature

199 Daily water temperatures (WT) in Bourgneuf Bay were calculated between
 200 January 1970 and December 2006, using the following regression (Haure and Baud,
 201 1995):

$$202 \text{ WT} = 0.8703 \times \text{AT} + 0.036 \times \text{TC} - 0.0969$$

203 Daily atmospheric temperatures (AT) were obtained from Météo-France's
 204 Climathèque database (Noirmoutier station, $2^{\circ}15'24''\text{W}$, $47^{\circ}00'18''\text{N}$) and tidal
 205 coefficients (TC) using the Marées dans le monde 2.02© software.

198 2.7. Statistical analysis

1
2
3 199 Sigmatat 3.1 (Systat software) was used to check the normality and
4
5 200 heteroscedasticity of data distributions and then to perform statistical analyses.
6
7
8 201 Temporal and spatial variations of environmental factors were compared by Student
9
10 202 t-tests or two-way parametric ANOVA, while correlation between them was
11
12 203 determined by Spearman correlation tests. Analyses of data from histological
13
14 204 determinations, as well as larval and post-larval cumulative densities, were first
15
16 205 performed with two-way parametric ANOVA within each reproductive cycle, and a
17
18 206 *posteriori* by Student-Newman-Keuls (SNK) tests.
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26 208 3. Results

29 209 3.1. Environmental variations

32 210 3.1.1. Seston quantity and quality

35
36 211 Over the sampling period, SPM, POM and chl-*a* concentrations were always
37
38 212 higher at the HT site compared to the IT site (Fig. 2A, B and C - two-way ANOVA, $p <$
39
40 213 0.01). The monthly mean POM:SPM ratio, used to estimate potential food dilution,
41
42 214 was lower at the HT site in 2005 and 2006 (Fig. 3A, t-test, $p <$ 0.01). On the other
43
44 215 hand, the monthly mean chl-*a*:POM ratio, used to estimate food quality, was higher at
45
46 216 the HT site in 2005 (Fig. 3B, t-test, $p <$ 0.01), while no significant difference between
47
48 217 sites was reported in 2006 (Fig. 3B, t-test, $p =$ 0.98).
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53 218

56 219 3.1.2. Fine-scale variations of water temperature and salinity: 2005 - 2006

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

228

229 3.1.3 Historical variations in water temperature

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

239

240 3.2. Microscopic determinations and oocyte size

241 Variations in oocyte size allowed identification of two distinct seasonal
242 reproductive cycles in 2005 and 2006 (Fig. 5). In 2005, no significant difference was

243 observed for mean oocyte diameter in intra-site (two-way ANOVA, $p = 0.85$) and
244 inter-site (two-way ANOVA, $p = 0.81$) comparisons. Similarly, in 2006, no significant
245 difference was observed for mean oocyte diameter in intra-site (two-way ANOVA, $p =$
246 0.84) and inter-site (two-way ANOVA, $p = 0.94$) comparisons. In both years, the
247 oocyte growth stage began in the same periods (end of March – beginning of April).
248 However, the mature stage, corresponding to the dominance of ready-to-spawn post-
249 vitellogenic oocytes in the gonads, was reached more quickly in 2006 than in 2005
250 (two vs. three months). Gonads entered a degenerating stage (evidence of atresia in
251 unspawned oocytes such as cell size increase and clearer cytoplasm – Dutertre et
252 al., in revision), more prematurely in 2006 than in 2005 (July vs. August,
253 respectively).

3.3. D-larva and post-larval densities

256 Cumulative D-larva densities showed significant differences related to both year
257 and site (Figs. 6 and 7, two-way ANOVA, $p < 0.05$ and $p < 0.01$, respectively).
258 Cumulative D-larva densities were higher at the HT site for both years (SNK-tests, p
259 < 0.05 for 2005 and $p < 0.01$ for 2006). For the IT site, cumulative D-larva densities
260 were higher in 2006 compared to 2005 (SNK-test, $p < 0.05$), while, for the HT site, no
261 significant differences were observed between the two years (SNK-test, $p = 0.30$). At
262 both sites, D-larvae appeared at the same periods: over two months in 2005, from
263 the beginning of July to the beginning of September, with a marked increase of the
264 planktonic larva densities observed at the end of August at the HT site. In 2006, the
265 HT site showed two main peaks of planktonic larva densities, at the end of July and

266 at the beginning of August, while, at the same periods, two smaller peaks of D-larva
267 densities were recorded at the IT site.

268 Cumulative natural post-larval recruitment also showed significant differences
269 related to both year and site (Figs. 6 and 7, two-way ANOVA, $p < 0.01$). Natural
270 recruitment was much higher in 2006 compared to 2005 at both sites (SNK-tests, $p <$
271 0.001 for the HT site and $p < 0.05$ for the IT site). Inter-site differences in the monthly
272 post-larval counts were also evident, with proportionately higher counts at the HT site
273 in both 2005 and 2006.

274 4. Discussion

275 4.1. Water temperature and recent oyster invasion

276 At approximately 28000 t, the feral oyster stock in Bourgneuf Bay equals 70%
277 of the annual farmed oyster production (Cognie et al., 2004; Martin et al., 2004;
278 2005). Water temperature variations, since the introduction of *C. gigas* for
279 aquaculture, clearly show that the onset of the feral oyster invasion coincided with a
280 marked water warming (Fig. 4). Indeed, between 1970 and 1995, when annual mean
281 water temperature was usually lower than the median temperature (13.4°C),
282 cumulative feral oyster recruitment was very low (Le Borgne et al., 1973; Gruet et al.,
283 1976; Gouletquer, 1995). Massive recruitment of feral oysters, observed since 1995
284 (Cognie et al., 2006) corresponded to the beginning of the period where summer
285 months often showed water temperature higher than 20°C , which is required for
286 successful *C. gigas* larval development in hatcheries (Arakawa, 1990; Shatkin et al.,
287 1997; Chávez-Villalba et al., 2002; Rico-Villa et al., 2008). These quantitative
288

289 historical data thus support earlier hypotheses of a relationship between *C. gigas*
290 proliferation in cool temperate European ecosystems and global warming (Diederich
291 et al., 2005; Ruesink et al., 2005; Smaal et al., 2005). Among the temperature-
292 related variables which could contribute to this proliferation are those which chiefly
293 affect larval survival and subsequent recruitment of feral oysters: oocyte reserves,
294 spawning period and seston conditions (Baldwin and Newell, 1995; Powell et al.,
295 2002; Chávez-Villalba et al., 2003; Rico-Villa et al., 2008).

296

297 **4.2. Oocyte fate timed by water temperature thresholds**

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

313 Similar oocyte size in farmed and feral oysters at both sites indicated that future
1 fertilized eggs would contain equivalent amounts of vitellus for the endotrophic and
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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).

319

320 4.3. Planktonic larval life

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

333

334 4.4. Feral oyster recruitment

335 Natural post-larval recruitment at both HT and IT sites was much higher in 2006
336 (4540 and 1489 annual settled post-larvae. m⁻², respectively) compared to 2005 (45

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

350

351 5. Conclusion

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

361 should thus produce an intensification of this proliferation, and a range extension
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2 362 northward in shallow European bays, including those used for oyster farming. Given
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4 363 the now near-ubiquitous distribution of *C. gigas* in temperate coastal habitats, these
5
6 364 observations should serve to alert the marine environment research community to
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9 365 potentially similar situations worldwide.
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534 **Fig. 1.** Location of northern (La Coupelasse) and southern (Gresseloup) oyster
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2 535 sampling sites (Δ) in Bourgneuf Bay. The intertidal zone and rocks are represented
3
4 536 by gray and black areas respectively (modified from Barillé et al., 2000).
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8 537 **Fig. 2.** Variations of suspended particulate matter (SPM, A), particulate organic
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10 538 matter (POM, B) and chlorophyll-a (chl-a, C) concentrations, and water temperature
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12 539 (D) at the northern high turbidity (HT) and southern intermediate turbidity (IT) sites of
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14 540 Bourgneuf Bay, in 2005 and 2006. Means \pm 95 % confidence intervals.
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18 541 **Fig. 3.** Dilution (POM:SPM, A) and quality (chl-a:POM, B) of organic particles at
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20 542 northern high turbidity (HT) and southern intermediate turbidity (IT) sites of
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22 543 Bourgneuf Bay in 2005 and 2006. Chl-a: chlorophyll-a, POM: particulate organic
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24 544 matter, SPM: suspended particulate matter. Means \pm 95 % confidence intervals.
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29 545 **Fig. 4.** Annual mean and warmest month mean of water temperature since the
30
31 546 introduction of *Crassostrea gigas* in the 1970's (Météo-France, Climathèque
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33 547 database, Noirmoutier, 2007), and relationship with the natural recruitment of feral
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35 548 oysters in Bourgneuf Bay (Gouletquer, 1995; Cognie et al., 2004; 2006; Martin et al.,
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37 549 2004; 2005). Dotted line corresponds to the median temperature (13.4°C) of annual
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39 550 mean water temperature, dashed line corresponds to the minimal threshold (20°C)
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41 551 for optimal *C. gigas* larval development.
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46 552 **Fig. 5.** Mean oocyte diameters (\pm 95% IC) for feral and farmed oysters, *Crassostrea*
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48 553 *gigas*, at northern high turbidity (HT, A) and southern intermediate turbidity (IT, B)
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50 554 sites of Bourgneuf Bay in 2005 and 2006.
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555 **Fig. 6.** D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity
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2 556 (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year
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8 558 **Fig. 7.** D-larva (A, C) and post-larval (B, D) densities at the northern high turbidity
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10 559 (HT) and southern intermediate turbidity (IT) sites of Bourgneuf Bay for the year
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	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

Table 1. Mean daily amplitudes (\pm 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.

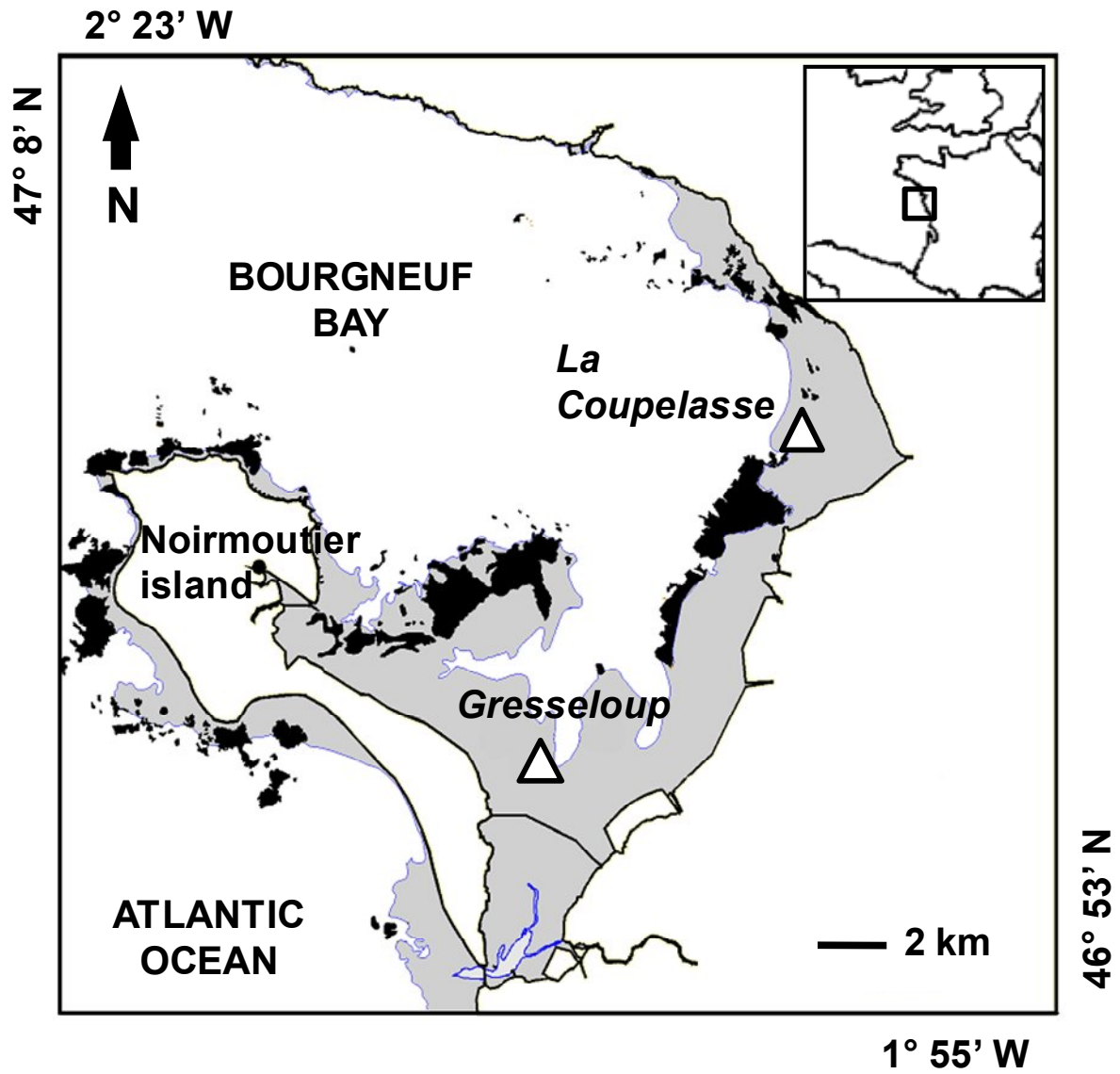


Fig. 1

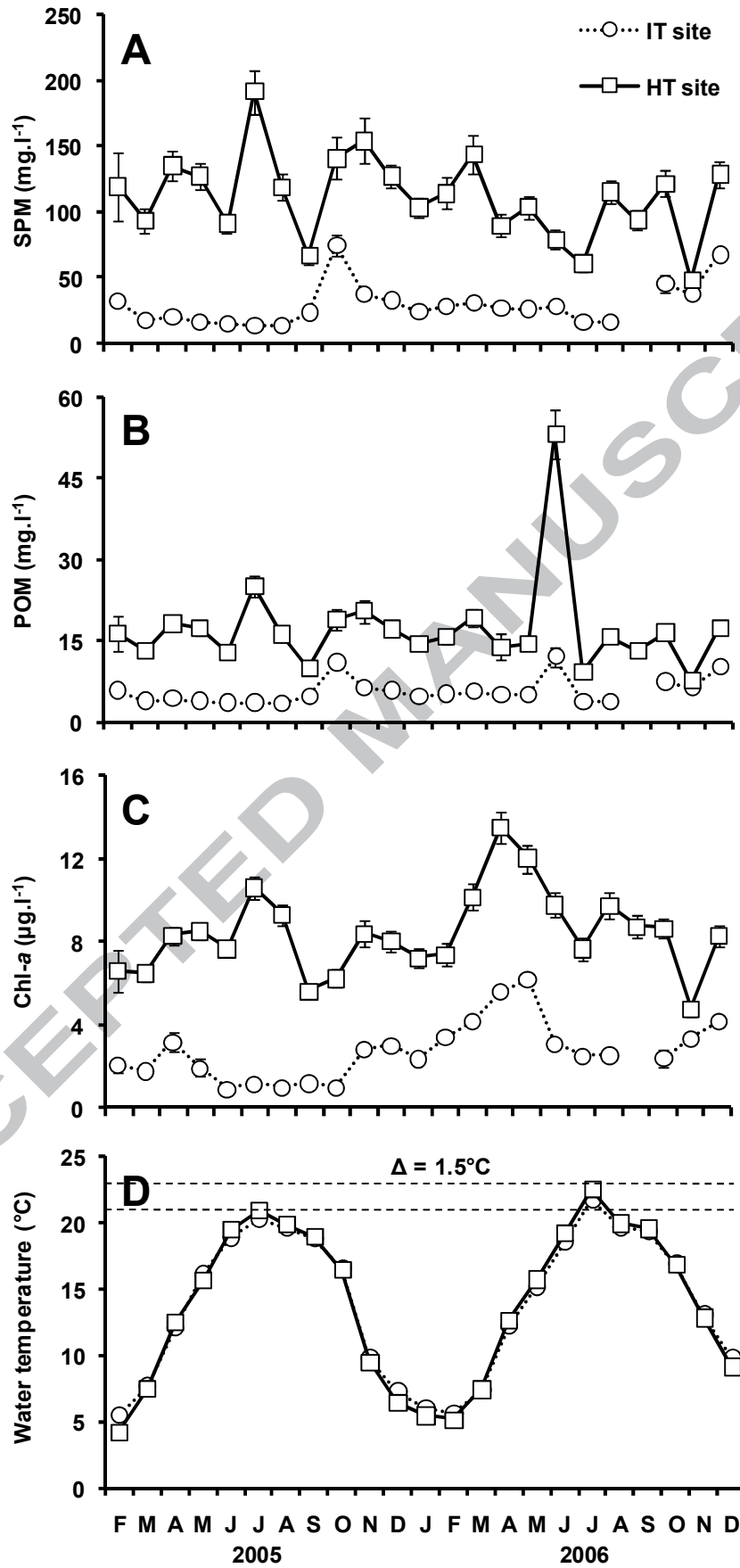


Fig. 2

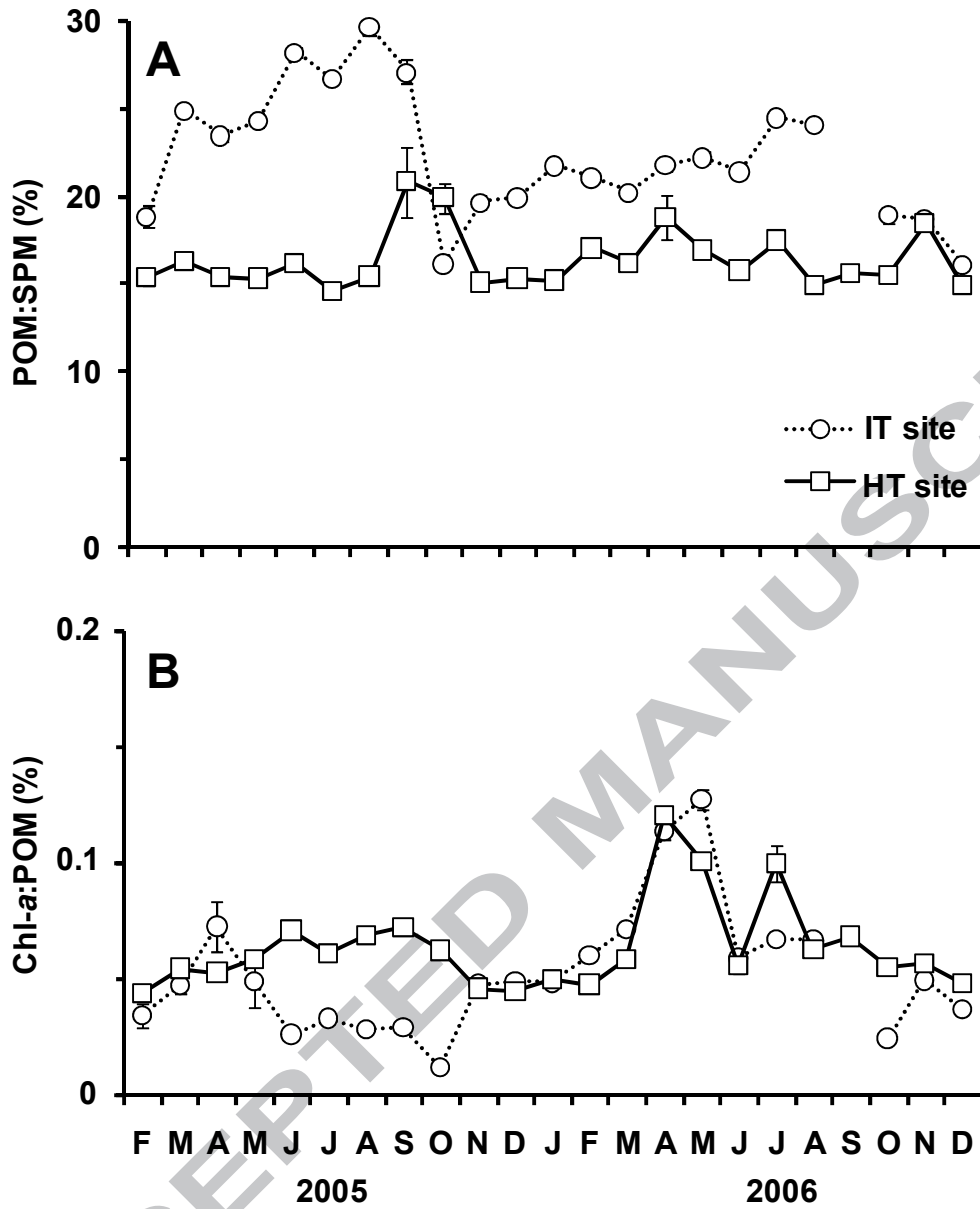


Fig. 3

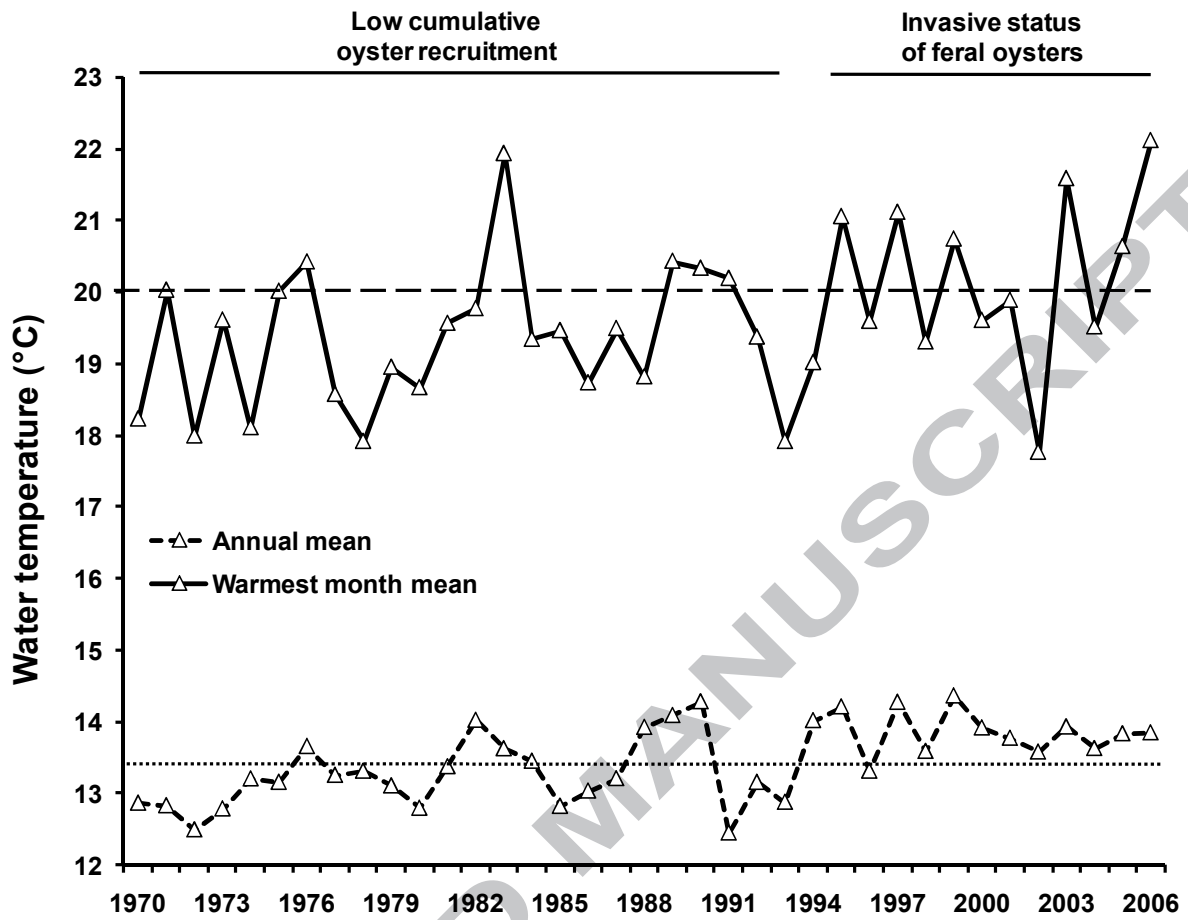


Fig. 4

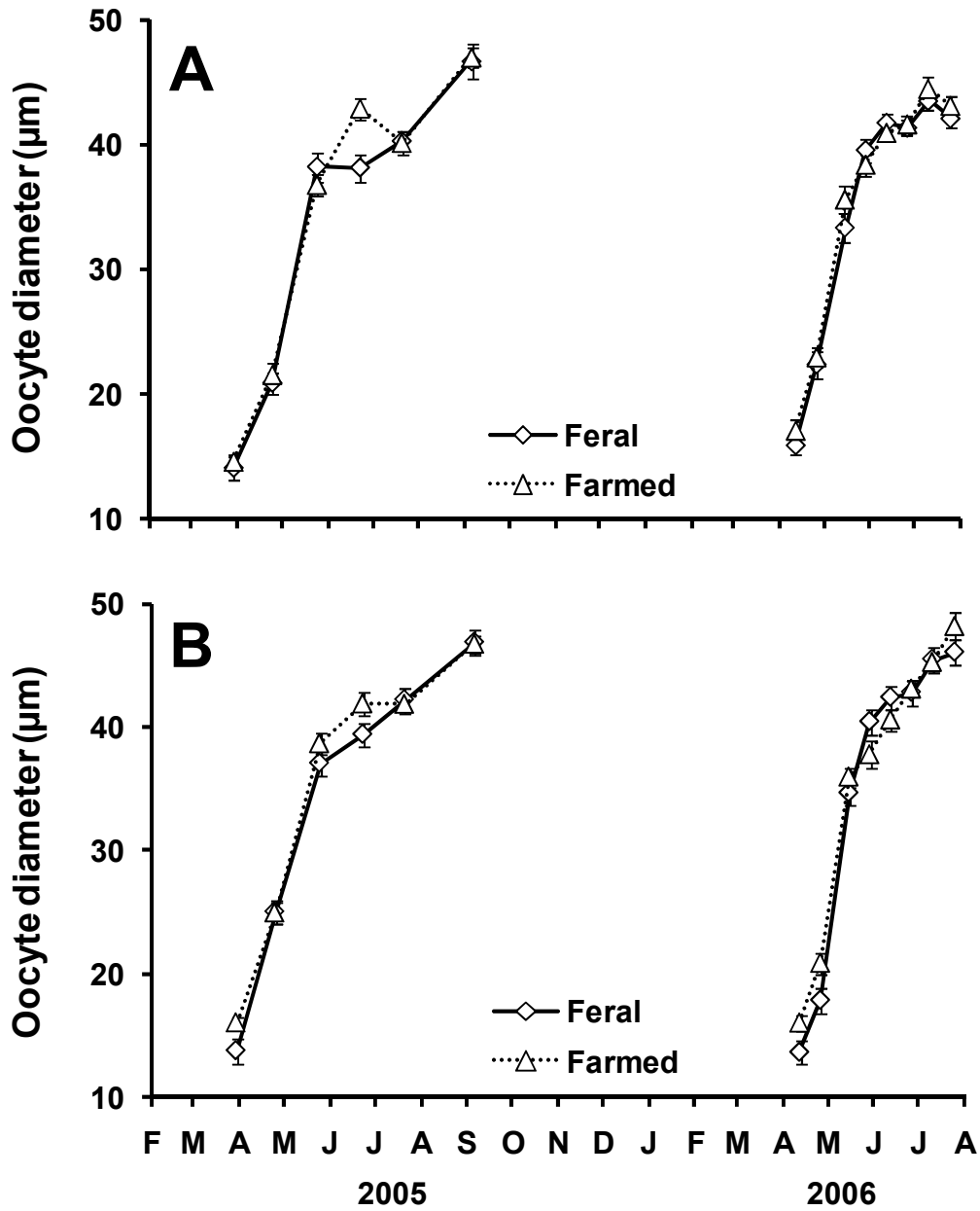


Fig. 5

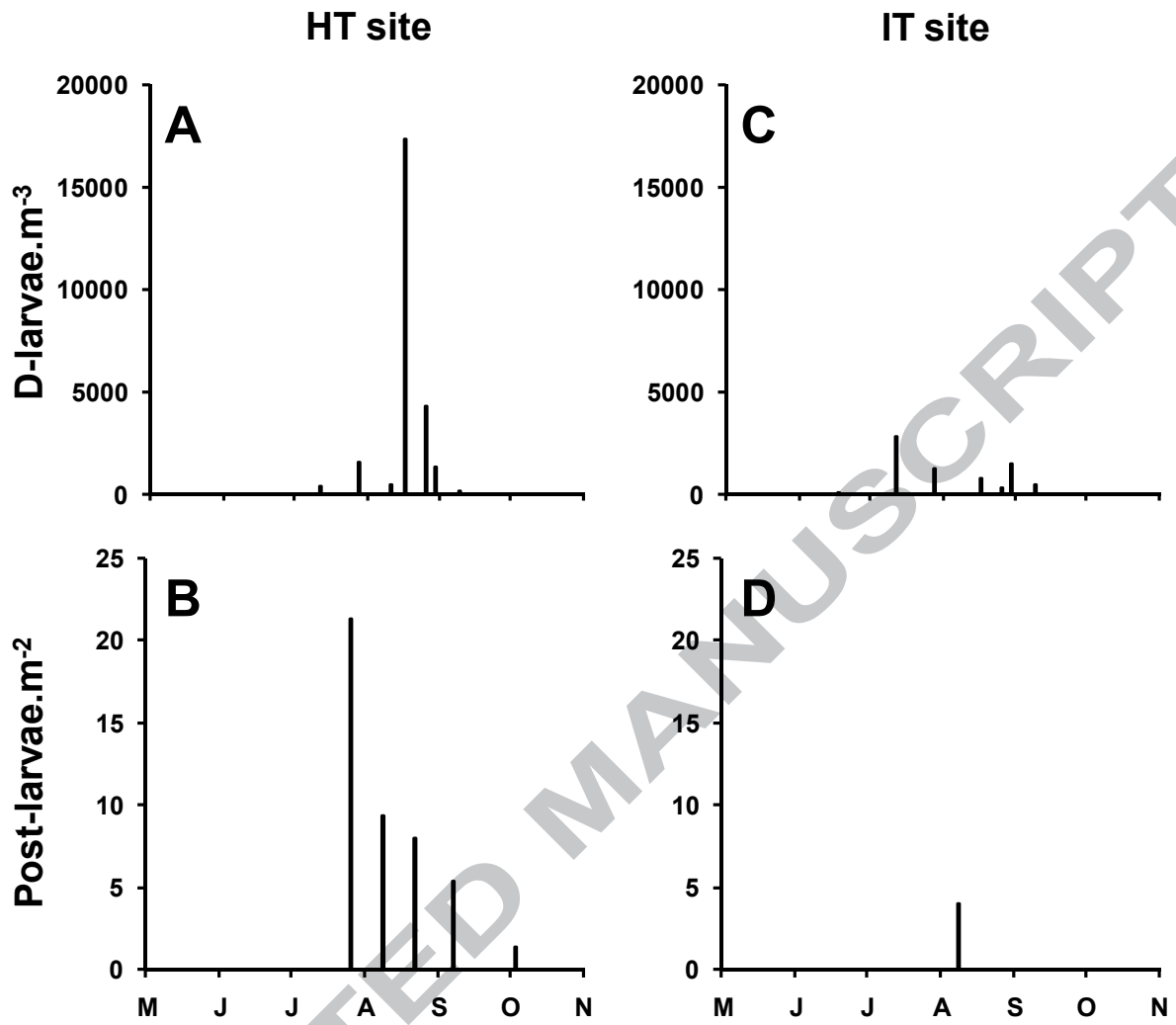


Fig. 6

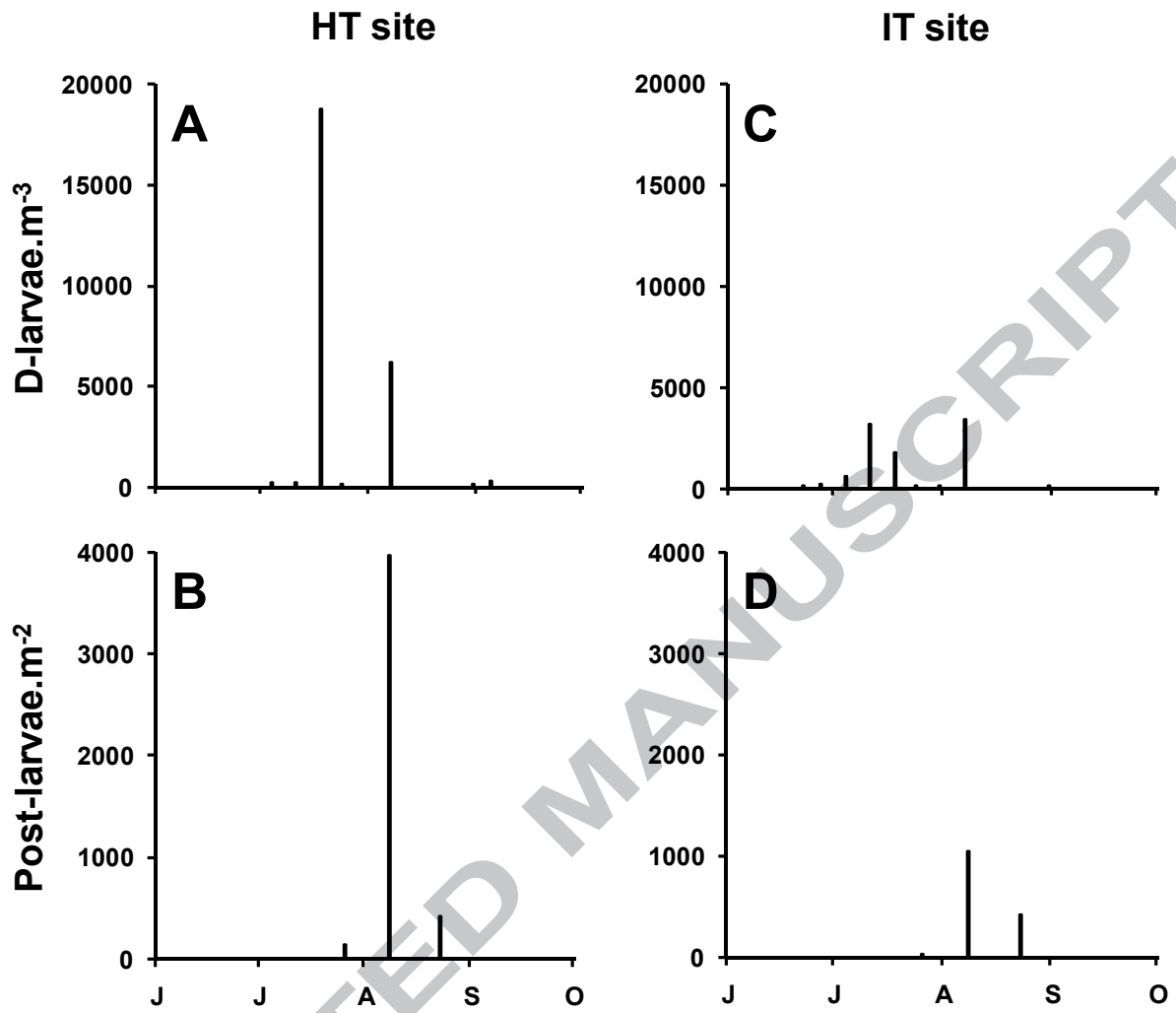


Fig. 7