The Manila clam population in Arcachon Bay (SW France): Can it be kept sustainable?

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Abstract:

The venerid clam *Ruditapes philippinarum* is the most prominent suspension-feeding bivalve inhabiting muddy intertidal seagrass beds in Arcachon Bay (SW France). It is exploited by fishermen, and Arcachon Bay ranks number one in France in terms of production and total biomass of this species. Previous studies revealed a decrease in the standing stock of *R. philippinarum* since 2003 and unbalanced length–frequency distributions with a lack of juveniles and of adults > 40 mm. Consequently, the population dynamics of this bivalve were studied at four intertidal sites and one oceanic site in Arcachon Bay. As clam size structure did not allow classical dynamics computations, field monitoring was coupled with field experiments (tagging–recapture) over two years. Monitoring of condition index and gonadal maturation stages highlighted a high variability in spawning number and intensity between sites. Recruitment events in the exploited area varied spatially but with uniformly low values. Von Bertalanffy Growth Function (VBGF) parameters (K, L_∞) were determined using Appeldoorn and ELEFAN methods. In the exploited sites in the inner lagoon, K was relatively high (mean = 0.72 yr^{-1}) but L_∞ was low (mean = 41.1 mm) resulting in a moderate growth performance index ($\Phi' = 2.99$). Growth parameters were not correlated with immersion time and L_∞ was different between sites. Comparison of mortality coefficients (Z) between cage experiments and field monitoring suggested that fishing accounts for 65–75% of total adult mortality. Low recruitment, a low growth rate and a normal mortality rate led to low somatic production (4.1 and 8.7 g Shell-Free Dry Weight (SFDW) m^{-2} yr^{-1}) and an annual P/B ratio from 0.44 to 0.92 yr^{-1}. Under current conditions, the possibility of a sustainable population in Arcachon Bay will strongly depend on recruitment success and fishing management.

Keywords: Manila Clam; *Ruditapes philippinarum*; Growth; Mortality; Reproduction; Population Dynamic; Production; Productivity

1. Introduction

The Manila clam *Ruditapes philippinarum*, endemic in Indo-Pacific waters, is one of the most commercially exploited bivalve mollusks in the world. Its high adaptability to various coastal environments makes this clam a very suitable species for aquaculture. Introduced to different parts of the world along with Pacific oyster *Crassostrea gigas* seed, the Manila clam is now widely distributed along the Pacific coast of the United States, the European Atlantic coast, the Adriatic and Aegean seas and the Indo-Pacific region (Jensen et al., 2004). *R. philippinarum* was introduced in Europe at the beginning of the 1970s for culture purposes, initially to France (1972) and later to England, Spain and Italy (Flassch and Leborgne, 1992). This species naturalized in all these countries and became a new commercially exploited resource.

In Arcachon Bay, the Manila clam was introduced in 1980 in designated growing areas as a commercially attractive species. *R. philippinarum* reproduced successfully in Arcachon Bay and rapidly naturalized in intertidal sea-grass beds (*Zostera noltii*) (Goulletquer et al., 1987). Today, Arcachon Bay ranks first in France in terms of national production and total biomass among surveyed stocks. In 2007, fishermen harvested around 1000 metric tons (Caill-Milly et al., 2008). The minimum catch size of individuals permitted by the European Union was originally 40 mm. In 2007, the catch size was decreased to 35 mm.

To control the fishing effort and to create a sustainable fishery, three Manila clam standing stock studies that were carried out in Arcachon Bay highlighted an estimated total stock of 8095 mt in 2003, 7307 mt in 2006 and 4865 mt in 2008 (Caill-Milly et al., 2003; 2006; 2008). These studies showed that since 2003, total and exploitable (> 35 mm) standing stocks have been decreasing. Furthermore, in these three studies, the length-size frequency distributions were characterized by a lack of juveniles and an absence of clams larger than 40 mm. The lack of juveniles could be the consequence of a default of gonadal maturation and/or of spawning, a high larvae mortality, or a recruitment deficiency. Two hypotheses could explain the lack of clams with > 40-mm shell length: 1) larger clams were removed by fishermen; 2) clams are not growing over 40 mm. In 1993, a study on reproduction and growth was carried out exclusively in clam growing areas (Robert et al., 1993). The lack of knowledge on *R. philippinarum* population dynamics in Arcachon Bay was the motivation for this study.

The present study focused on the population dynamics of the Manila clam in its natural habitat, muddy intertidal flats, at Arcachon Bay. The aim of this study was to provide reliable population dynamics parameters in terms of growth, mortality and reproduction in order to implement a fishing strategy model (Bald et al., in revision). These data allowed us to calculate the production and the productivity (P/B = production/biomass ratio) of the clam population. One of the greatest difficulties was that clam population size structure did not permit classical dynamics analyses due to the difficulty in identifying cohorts, as already mentioned by Ramón (2003). Consequently, field monitoring was coupled with field experiments involving individual tagged clams in enclosures (tagging-recapture method).

2. Material and Methods

2.1. Study sites

Arcachon Bay is a 180-km^2 semi-sheltered lagoon on the southwest coast of France (Fig. 1). The inner lagoon includes 110-km^2 of mudflats that are colonized by a vast *Zostera noltii* seagrass bed. The Manila clam *Ruditapes philippinarum* is, in terms of biomass, the dominant species of these intertidal flats (Blanchet et al., 2004). Arcachon Bay receives freshwater inputs mainly by the Leyre River and marine water via two channels located at the southwest end of the lagoon. These fresh and oceanic water inputs as well as the slow renewal of water by tides (Plus et al., 2006) induce salinity and temperature gradients within

the bay (Bouchet, 1968). Water salinity and sediment temperature of the Manila clam habitat vary from 4 to 35 psu and from -2 to 44°C, respectively (Dang et al., 2008). Sediment composition is mud to muddy sands. Four sites were investigated in the inner part of the bay: Ile aux Oiseaux, Andernos, Gujan and Lanton; another site, Arguin, is located in the oceanic part of Arcachon Bay in the National Reserve of Banc d'Arguin (Fig. 1).

2.2. Environmental parameters

Sediment grain-size, sediment organic matter and elevation above chart datum (CD) were measured at each of twenty cage locations at the end of 2006. Elevation above CD corresponds to the height (in meters) of the bottom surface. The ten first centimeters of the sediment were sampled by a 5 cm-diameter corer and frozen until analysis. Sediment granulometry was determined using a laser-diffractometer Malvern Master Sizer. This device uses the properties of diffraction and diffusion of particles with a laser beam. Total organic matter in the sediment was obtained by calcination (550°C, 2h). Water salinity was provided by Auby et al. (1999). Topographic surveys were conducted using a DGPS (Trimble 5700) with an accuracy of about 2.5 cm in the horizontal and 2 cm in the vertical. Immersion time was calculated from a tidal curve (tide height in meters *vs* time in hours) with a mean tidal coefficient of 63. Sediment temperature was measured with a Prosensor Thermic Tidbit probe (period = 1 hr, precision 0.4°C) at a single station per site (Arguin 2, Ile aux Oiseaux 2, Andernos 4, Gujan 3 and Lanton 3) from December 2005 to October 2007. The choice of sediment temperature instead of water temperature was motivated by a previous study comparing both temperatures between January and September 2006 (N =5847).This comparison showed that the mean temperature was identical, but that sediment temperature underlined higher minimum and maximum value, that are undergone by clams and that are more realistic for these intertidal organisms. Data were collected regularly with an infrared optic shuttle and transferred to a PC with BoxCar Pro (version 3.51 for Windows) software.

2.3. Population size structure and reproductive patterns

Length-frequency data of the Manila clam population ambient the enclosures at Ile aux Oiseaux (November 2005 to September 2007) and at Andernos (October 2005 to September 2007) were assessed. These two sites were selected because their clam abundance is considered as 'representative' of the lagoon (Bertignac et al., 2001; Caill-Milly et al., 2003). Every other month, sampling consisted of collecting the top 15 cm of sediment (surface: 0.25-m^2) along a transect line (500 m) at each of ten stations established every 50 m, the first station being randomly selected. The sediment was sieved through a 1-mm mesh and *R. philippinarum* individuals were subsequently isolated in the laboratory and their shell lengths measured for assignment to size-classes from 6 to 44 mm.

In order to assess the reproductive patterns of *R. philippinarum* in Arcachon Bay, thirty clams from 30 to 40-mm shell length were sampled monthly over one year at Ile aux Oiseaux (December 2005 - February 2007) and Gujan (February 2006 - February 2007); and during two years at Andernos (December 2005 - October 2007) and Lanton (December 2005 - October 2007). Clams were dissected and their condition index was evaluated separately for males and females, to assess spawning synchronicity, as

$$CI\ (\text{‰}) = dry\ flesh\ weight\ (mg) / dry\ shell\ weight\ (g)$$ (Walne and Mann, 1975).

During clam dissection, gonad development stage according to the macroscopic scale proposed by Lucas (1965) was estimated under a stereomicroscope. In stage A, the gonad is translucent and sex is not identifiable. In stage B, the sex is sometimes detectible and gonads are translucent to whitish and show the early stages of maturation. Gonads of clams in stage C are totally mature and strongly developed, with numerous spermatozoa and oocytes. Individuals may potentially spawn (in one or successive events) and remain in stage C. The gonad is whitish and inflated. When the gonad is completely empty of gametes (stage D), it becomes brown, wrinkled and flaccid. This stage can last few months. When possible,

the sex ratio, i.e. number of females / number of males was determined for each date at each site.

2.4. Growth transplant experiment

Clams with shell-lengths between 6 and 44 mm were collected at Ile aux Oiseaux in November 2005. Each individual was labeled with a numbered tag and measured to the nearest 0.1 mm shell length before being released into different enclosures. Four enclosures were placed at each site (Arguin, Ile aux Oiseaux, Andernos, Gujan and Lanton), each one located at a different elevation from enclosure 1 (lowest level) to enclosure 4 (highest level). Each enclosure consisted of a 50 cm length x 50 cm width x 20 cm height topless metal frame meshed with a 2-mm plastic net, buried 15 cm into the sediment, projecting 5 cm into the overlying water column and anchored with iron bars. The sediment within the enclosure was flushed level with the surrounding sediment. We considered that enclosures just represented a barrier from which clams could be retrieved but which had little effect on local environmental conditions (grain size and grass-cover remained identical than outside the enclosure). Compared to the surrounding condition, enclosures were not considered as confounding treatments (Underwood, 1997). All enclosures were emptied of native clams before the experiment. Clam density in each enclosure was 320 ind. m^{-2} and the biomass was 24.2 g Shell-Free Dry Weight (SFDW) m^{-2}. These represented higher values than the average in Arcachon Bay. However, such densities and biomass were locally observed (Blanchet et al., 2004; Caill-Milly et al., 2008). *R. philippinarum* were seasonally recaptured and their shell length was measured over a total period of two years. The obtained size increments were used for the estimation of growth parameters (see 2.5.1).

2.5. Data analysis

2.5.1. Growth

Von Bertalanffy growth function (VBGF) $L(t) = L_\infty[1 - \exp[-K(t - t_0)]]$ predicts length as a function of age and is commonly used in bivalve growth analysis (Bourne, 1982; Maronas et al., 2003, Fiori and Morsan, 2004; Peharda et al., 2007). This particular function was used in our work in order to allow comparisons with previous studies. L_∞ is the asymptotic shell length (mm), K is the growth coefficient (yr^{-1}) and t_0 is the theoretical age at zero length (yr).
In the present study, two methods were used to determine VBGF parameters *i.e.* K and L_∞, both using FISAT II software (version 1.2.2, FAO-ICLARM).
The first method used the measurements taken during the growth transplant experiment, *i.e.* length increment data obtained from each of the five stations located at Arguin, Ile aux Oiseaux, Andernos, Lanton and Gujan (total of 20 stations). L_∞ and K were assessed using Appeldoorn's method (Gayanilo et al., 2005).
The second method used the length-frequency data obtained in the 2-yr population size structure monitoring study at Andernos 4 and Ile aux Oiseaux 2. VBGF parameters were determined using the non-parametric Electronic Length-Frequency Analysis I (ELEFAN) method. This approach evaluates the best K/L_∞ pair by assessing Rn coefficient (Pauly and Moreau, 1997). $R_n = (ESP/ASP) \times 1000$, ESP is the Explained Sum of Peaks and ASP is the Availables Sum of Peaks. A higher Rn value indicates a better fit between the components and growth curve. Limits of K and L_∞ values entered in FISAT were set at 0.4 to 1.3 yr^{-1} and 36 to 45 mm respectively.
The growth performance index (Φ') (Pauly and Munro, 1984) was calculated using K and L_∞

using the following equation:

$$\Phi' = 2Log(L_\infty) + Log(K)$$

2.5.2. Mortality

In the same way as growth parameter determination, mortality rate Z was estimated using data from the growth transplant experiment and the population size structure monitoring. Mortality is the result of the decrease of abundance, generally expressed as $N_t = N_0\,e^{-Zt}$ where N_0 is the number of individuals at relative age 0 and t is the relative age, which is usually close to one year.

First, in each cage, the number of clams at experiment completion was compared to the number of clams at start. Mortality was related to shell length at the experiment's start, using tagged shell figures. Because of low number of individuals, clams were pooled by 4-mm shell length size classes to calculate a percentage of mortality throughout the duration of the experiment. Knowing shell growth (VBGF), it was consequently possible to plot a mortality curve $Ln\,N_t = -Zt$ and to estimate the mortality coefficient Z. N_t is the abundance (ind) at relative age t, t is the time (yr) and Z is the mortality constant (yr^{-1}). At each station, Z was calculated for two intervals of clam shell lengths, 4-20 mm and 20-40 mm, in order to compare results with the ELEFAN method.

Second, the instantaneous total mortality coefficient Z was estimated from the 2-yr population structure monitoring at Andernos and Ile aux Oiseaux. This approach consisted of using the length-catch curve converting method (Pauly, 1983) of the FISAT II software (version 1.2.2, FAO-ICLARM) and the single negative exponential mortality model (Gayanilo et al., 2005). Lengths of pooled length-frequency samples were converted into ages with parameters of the VBGF. Mortality was calculated by linear regression analysis.

The curve was constructed by plotting the adjusted frequencies (N) of clams in each length-class (i.e. log (N/Δt)) against the length-converted mean relative age (t) (Pauly and Moreau, 1997). The 2006 and 2007 years of the survey were considered together and VBGF parameters used were those calculated by Appeldoorn's method for Andernos 4 and Ile aux Oiseaux 2, which were the nearest enclosures.

2.5.3. Biomass, production and productivity

The annual mean biomass, the annual somatic production and the P/B ratio were evaluated from the population size structure monitoring for Manila clam populations at Andernos (immersion rate: 60-70%) and Ile aux Oiseaux (immersion rate: 45-50%) in 2006 and 2007. Utilized VBGF parameters (K and L_∞) were those obtained by the growth transplant experiment at Andernos 4 and Ile aux Oiseaux 2 (Appeldoorn's method) that were the nearest enclosures. In order to calculate production and biomass, the specific relationships between shell length, dry flesh weight and shell weight were estimated. Consequently, one hundred clams from 7 to 41 mm were collected at Andernos. Their dry flesh weight and shell length were evaluated to finally obtain the following equation:

$$log_{10}SFDW = -5.523 + 3.22\,log_{10}L \quad \text{(g)} \quad (R^2 = 0.93)$$

SFDW is the shell-free dry weight (g) and L corresponds to the shell length (mm).

The mean annual biomass was formulated by the following equation:

$$B = \sum N_i M_i \quad \text{(g SFDW. m}^{-2})$$

N_i and M_i are the mean number of animals per m^2 and the mean individual somatic mass in size class i.

The total annual production was calculated according to the mass specific growth rate method (Brey, 2001) from the size mass relation, the VBG equation and the pooled size-frequency distribution:

$$P = \sum N_i M_i G_i \quad \text{(g SFDW. m}^{-2}\text{. yr}^{-1}\text{)}$$

G_i is the mass specific growth rate, which is represented by:

$$G_i = b\,K\,(L_\infty - L_i)/L_i \quad \text{(yr}^{-1}\text{)}$$

b (= 3.22) is the specific constant of the size mass relation, K and L_∞, are the VBGF parameters and L_i is the mean size of class i.

The annual P/B ratio of *R. philippinarum* populations were evaluated from annual total production and annual mean biomass.

2.5.4. Statistical analysis

To compare condition index (CI) between months at each site, Kruskal-Wallis non-parametric test was used (Statistica software). Maximum type I error rates were set at α = 0.05. When difference was significant, a non parametric post hoc test was performed between highest and lowest values of CI in order to detect praks (prespawning period) from spent or rest period.

Two way Anova tests were realized to compare differences between condition index of both sexes (factors: months and sexes). When difference was significant, a post hoc test of Tukey was achieved. To evaluate a possible difference of sex ratio at each site, Chi2 test were performed.

Finally, in order to test whether the elevation above chart datum and the sites have influence over clam growth parameters (K and L_∞ and Φ'), we used the non-parametric Kruskal-Wallis test with SAS software. When Kruskal-Wallis tests indicated a significant heterogeneity between treatments, a non-parametric version of the SNK test based on the sums of ranks was used to compare treatments two by two.

3. Results

3.1. Environmental parameters

The elevation above chart datum CD was determined for each station of the 5 sites (Table 1). The lowest station was at 0.8 m (Lanton 1) and the highest station at 2.8 m (Arguin 4), which corresponded to an immersion time ranging from 96% to 38% respectively (Table 1). Grain-size analysis discriminated Arguin (medium sand, median = 360 μm) from the four other sites (muddy sediments, median = 50-160 μm) located in the inner part of Arcachon Bay (Table 1). Arguin displayed the lowest values of sediment organic matter (1%) and sediment silt (3.5%) whereas the Lanton site inside the lagoon reached 8.5 ± 3% and 41 ± 12.9% respectively. Daily mean sediment temperature for the five sites was monitored (Fig. 2). Arguin differed from other sites by reduced seasonal variability, *i.e.* lower temperatures in summer and higher temperatures in winter (Fig. 2). Sediment minimum temperatures varied between 0.2°C (Ile aux Oiseaux) and -1.7°C (Lanton), maximum temperature between 30°C (Arguin) and 43.7°C (Gujan), and mean temperature between 15.1°C (Arguin) and 16.1°C (Ile aux Oiseaux) (Fig. 2). Minimum water salinity ranged between 4.8 (Lanton, Gujan) and 32.2 (Arguin), maximum salinities between 26.7 (Lanton, Gujan) and 34.2 (Arguin). Thus, Arguin was the most stable site in terms of sediment temperature and water salinity; Lanton and Gujan displayed the highest variability.

3.2. Reproduction

Clam reproduction was followed through condition index (CI) and gonadal maturation stages (Fig. 3, 4). In all sites, clam CI fluctuated with lowest values in winter and highest values in spring and summer (Fig. 3). Kruskal-Wallis tests revealed significant differences of CI with time at the four studied sites ($P < 0.005$ for the four sites). Then, post hoc tests comparisons allowed determining peaks. In 2006, clams from Andernos and Gujan exhibited the highest CI with a peak at 65‰, when Lanton and Ile aux Oiseaux reached 50‰. Peaks occurred in June and September at Andernos (Kruskal-Wallis (KW) post hoc test comparison, $P < 0.05$) (temperature (T°) = 22.2°C and 21.3°C, respectively), in May and July at Ile aux Oiseaux (KW post hoc test comparison, $P < 0.05$) (T° = 18.4°C and 25.6°C, respectively), in June at Gujan (KW post hoc test comparison, $P < 0.05$) (T° = 22°C) and in July at Lanton (KW post hoc test comparison, $P < 0.05$) (T° = 25.6°C). The decrease of CI related to the spawning period after the gonad was ripe, *i.e.* reproduction stage C (Fig. 4). Gametogenesis started in March (stage B), except in the inner station of Lanton where it occurred in April (Fig. 4). It coincided with a sediment temperature of 10°C. Spawning occurred from June to August and from September to October at Andernos; from May to June and from July to August at Ile aux Oiseaux; from June to August at Gujan; and from July to September at Lanton. In 2007, only Andernos and Lanton were monitored. At Andernos, peak CI was much lower than in 2006, when it was similar to that observed in Lanton. Maximum CI and spawning periods were similar in both years with a later maturation in the inner station of Lanton. As opposed to 2006, in Andernos, only one spawning occurred from July to September 2007. Temperatures were lower in 2007, with a temperature of 21.8°C at Lanton in July and 21.6°C at Andernos in July, than in 2006 when temperatures were 25.6°C and 25.7°C, respectively.

CI did not differ between males and females (two way Anova, $P > 0.05$) at the four studied sites but exhibited a significant different with time (two way Anova, $P < 0.05$) at Andernos, Lanton and Gujan, at the opposite of Ile aux Oiseaux (two way Anova, $P > 0.05$) with no significant interactions between sexes and months for all sites (two way Anova, $P > 0.05$) (Fif. 5). Differences in CI appeared between May and June 2006 at Andernos, between June and July 2007 as well as between July and August 2007 at Lanton, between May and June 2006 and between June and July 2006 at Gujan (post hoc test of Tukey, $P < 0.05$).

In 2006, mean sex ratios (number of females / number of males) ranged between 0.85 at Andernos ($P > 0.05$), 0.93 at Lanton ($P > 0.05$), 0.99 at Gujan ($P > 0.05$) and 1.23 at Ile aux Oiseaux ($P > 0.05$).

3.3. Growth

The first step consisted of calculating VBGF parameters (K and L_∞) in the twenty cages through the growth transplant experiment, using Appeldoorn's method (FISAT II software) (Table 1). No significant difference was found between VBGF parameters and elevations above chart datum (CD) at each site (Kruskal-Wallis test, $P > 0.05$). K did not vary between the five sites (Kruskal-Wallis test, $P > 0.05$). L_∞ was significantly different among all studied sites, except between Andernos and Gujan. Growth performance index Φ' did not differ between sites and between elevations above CD at each site (Kruskal-Wallis test, $P > 0.05$).

The second step consisted of determining VBGF parameters K and L_∞ through the length distribution data analysis with the ELEFAN I's method (FISAT II software) at Ile aux Oiseaux and Andernos. Length size frequency distributions are represented in Figure 6. These histograms show the scarcity of juvenile *R. philippinarum* at Ile aux Oiseaux and especially at Andernos, as well as the scarcity of adults > 40 mm, compared to the abundance of the clams of 28-40 mm in shell length. Few juveniles occurred in spring in March 2006 at Andernos and in April 2007 at Ile aux Oiseaux.

The best pairs K/L_∞ obtained by ELEFAN I were [1.03 yr^{-1}/37.8 mm] at Andernos and [0.81 yr^{-1}/37.8 mm] at Ile aux Oiseaux. The K value was similar to the one found by our growth

experiment (nearest enclosures: Ile aux Oiseaux 2 and Andernos 4) at both sites whereas the asymptotic length was lower.

3.4. Mortality

The first method of Z assessment was based on individual mortality in experiment enclosures. Z mortality coefficients varied between stations and length-classes but were generally < 1.5 yr^{-1}, except on two occasions (larger length-class at Ile aux Oiseaux 1 and 3) (Table 1).
The second estimation of Z was performed using the length-converted catch curve method (FISAT II) and the 2-yr population structure monitoring at Ile aux Oiseaux and Andernos. Size classes were determined following the size-converted catch curve and determination coefficient (Fig. 7). For both sites, the mortality rate was higher for juveniles than adults. At Andernos, mortality rate was Z = 5.83 yr^{-1} (R^2 = 0.74) for size classes 9-19 mm and Z = 1.41 yr^{-1} (R^2 = 0.98) for 33-38 mm clams (Fig. 6). At Ile aux Oiseaux, mortality rate was Z = 3.43 yr^{-1} (R^2 = 0.97) for size classes 8-20 mm and Z = 1.44 yr^{-1} (R^2 = 0.98) for adult clams of 30-37 mm (Fig. 7).

3.5. Biomass, production and productivity (P/B)

Mean annual clam abundance was 41.8 and 44.5 ind. m^{-2} at Andernos in 2006 and 2007 respectively, and for Ile aux Oiseaux it was 63.6 and 120.9 ind. m^{-2} in 2006 and 2007 respectively (Table 2). Difference between both sites was due to the higher abundance of juveniles at Ile aux Oiseaux. It represented mean annual biomass estimates of 9.3 g SFDW m^{-2} (2006) and 10.1 g SFDW m^{-2} (2007) at Andernos, and 5.8 g SFDW m^{-2} (2006) and 10.5 g SFDW m^{-2} (2007) at Ile aux Oiseaux (Table 2). The observed relationship between length and dry weight was used to estimate production. The somatic annual production assessed was 4.1 g SFDW m^{-2} yr^{-1} (2006) and 4.6 g SFDW m^{-2} yr^{-1} (2007) at Andernos, and 5.3 g SFDW m^{-2} yr^{-1} (2006) and 8.7 g SFDW m^{-2} yr^{-1} (2007) at Ile aux Oiseaux (Table 2). The distribution of total annual production P among the size classes is illustrated in Figure 8. The main part of production was supported by adult clams > 30 mm at Andernos (2006 and 2007) and Ile aux Oiseaux in 2007, whereas P was sustained by both juveniles and adults at Ile aux Oiseaux in 2006. Production of adults was higher for Ile aux Oiseaux in 2007 compared to 2006 and with Andernos in 2006 and 2007 (Fig. 8). P/B ratios were similar for both years at Andernos, around 0.45 yr^{-1}, and was slightly higher in 2006 (0.92 yr^{-1}) than in 2007 (0.82 yr^{-1}) at Ile aux Oiseaux (Table 1).

4. Discussion

This work was realized in the context of a strong decrease in the Manila clam stock in Arcachon Bay. Recent studies showed a deficit of juveniles and a lack of large clams up to 40 mm. The present work highlighted poor performance of the Manila clam population in terms of reproduction and growth. Indeed, gametogenesis displayed low values (analyzed through condition index evolution) and recruitment was poor (2006-7). Growth was characterized by an inability to surpass 40 mm shell length. Surprisingly, the K parameter was similar at all sites and levels above chart datum (CD), whereas L$_\infty$ differed between sites (not elevation above CD) but remained in a rather low range. This situation makes the sustainability of the stock most precarious, particularly in its present exploited context.
This study confirmed the observations of previous authors on the gametogenic cycle of the Manila clam, who found a high variability following geographical location (Drummond et al., 2006). Condition index is considered as a good indicator of the spawning period (Laruelle et al., 1994; Drummond et al., 2006; Toba et al., 2007). The maximum observed CI

corresponds to a peak in ripeness following an accumulation of resources in preparation for spawning (Drummond et al., 2006). In Arcachon Bay, spawning periods varied according to site and to year with a delay of one month between the inner station of Lanton and the three others. Clams spawned twice in 2006 and once in 2007 at Andernos, once at Lanton in 2006 and 2007, twice at Ile aux Oiseaux and once at Gujan in 2006. Consequently, this study revealed the spatial and temporal variability of spawning events at the kilometer scale within Arcachon Bay. A previous study on three sites located in Arcachon Bay showed that in 1990, a single autumn spawning period was recorded (Robert et al., 1993). Different studies around the world showed that *R. philippinarum* displays different periods of spawning by location (Table 3). In some cases, this period lasts for a few months as is the case in Venice lagoon (Meneghetti et al., 2004) or in the North-East Pacific (Holland and Chew, 1974; Bourne, 1982). No differences were revealed in spawning chronology between males and females, as previously reported for *R. philippinarum* from north-western France (Laruelle, 1999).

Temperature is a forcing variable for reproduction. In the present study, it was measured in the sediment because clams live in tidal flats and experience successively aerial and water influence. Manila clams have been found experimentally to begin gamete maturation when the temperature reaches 12°C, even if gametogenesis may start at 8°C (Delgado and Pérez-Camacho, 2007). This temperature threshold was confirmed by field observations (Ohba, 1959; Holland and Chew, 1974; Mann, 1979; Xie and Burnell, 1994). In the present study, maturation began in March when mean sediment temperature was 10.5°C in 2006 and 11.8°C in 2007. The lowest temperature limit for spawning is 14°C (Beninger and Lucas, 1984; Rodriguez-Moscoso et al., 1992). At Arcachon Bay, gonads started to ripen in April-May, depending on the site, when sediment temperatures reached on average 14.5°C and 16.6°C in April 2006 and 2007 respectively, as well as 18.5°C and 18°C in May 2006 and 2007, respectively. Most individuals were ripe during three months from May to July at Gujan and Ile aux Oiseaux and from June to August at Andernos and Lanton. Spawning events began at various sediment temperatures, *i.e.* 18.5 °C at the minimum (May 2006, Ile aux Oiseaux) and 25.6 °C at the maximum (July 2006, Lanton and Ile aux Oiseaux). Our results were in accordance with literature with a beginning of maturation at 10°C and with spawning at a temperature above 14°C. Even if it was an important factor in the determination of maturation and spawning periods, the variability of temperature during spawning in Arcachon Bay suggests that other environmental factors must be essential such as trophic sources (Laruelle et al., 1994) or salinity (proximity of the river) (Robert et al., 1993).

Clams size structure was unbalanced in Arcachon Bay as shown by histograms at Andernos and Ile aux Oiseaux as well as by previous campaigns that evaluated the standing stock in 2003, 2006 and 2008 (Caill-Milly et al., 2003; 2006; 2008). Size structure of the Manila clam was characterized by an absence of adults > 40 mm and by a deficit of juveniles, which was particularly alarming for the survival of the population and for the exploitation by fishermen. However, clams develop gametes at a clam shell length of 5-10 mm and reach maturity at 15-20 mm with all individuals over 20 mm able to spawn (Holland and Chew, 1974).

The lack of juveniles could be explained by three hypotheses: 1) Reproduction was not efficient enough to produce larvae. The amplitude of variation of the CI from reproductive to resting periods is representative of the spawning intensity. In the Laruelle et al. (1994) study, the CI was around 60‰ out of gametogenesis period, whereas maximum values reached 131‰ in the Bay of Brest and 142‰ in the Morbihan Gulf, against 66‰ in Arcachon Bay (and around 40‰ for the resting period). Consequently, the amplitude of CI variation was considerably higher in the two Brittany sites than in Arcachon Bay. Values observed in Morbihan Gulf were close to those observed in clams from Arguin, *i.e.* located in oceanic conditions (Dang, unpublished data). The small average length of adult clams in Arcachon Bay can also exacerbate larval depletion. 2) Larvae were produced but endured high planktonic mortality, due to unfavorable environmental conditions. Manila clam eggs require 1-2 days at a temperature of 13-16°C to hatch, followed by an optimal temperature of 25°C and salinity of 20-30 for larval survival (Robinson and Breese, 1984). For instance, insufficient temperatures were the reason for the non-recruitment of Manila clams in

Southern Ireland (Xie and Burnell, 1994). 3) Reproduction occurred, larvae survived but new recruits underwent mortality due to adverse environmental conditions (low temperatures in winter) and/or predation. The density of 2-3 mm shell length clams in the present study was under 23 ind. m^{-2} in April 2007 at Ile aux Oiseaux 2 and 4 ind. m^{-2} in March 2006 at Andernos 4. These values are catastrophic for population survival, when related to Ohba (1959) values of 2000 -2500 ind. m^{-2} for a length of 2-3 mm and to Humphreys et al. (2007), who found settlement densities were two orders of magnitude below those of Ohba (1959). Poor survival of recruits can be the consequence of many factors, including predation (Sanchez-Salazar et al., 1987; McArthur, 1998; Hiddink et al., 2002). The density of crabs in these seagrass beds can reach 23 ind. m^{-2} (Blanchet et al., 2004). The role of grazing by Brent Geese remains unknown. Secondary settlement and juvenile migrations are unlikely (de Montaudouin, 1997). Only two sites were sampled in this study but previous large-scale sampling campaigns collecting all size classes of clams > 5 mm found small amounts of juveniles (Caill-Milly et al., 2003, 2006, 2008). In addition, a 2002 survey involving 49 stations sieved with 1-mm mesh revealed a lack of juvenile clams (Blanchet et al., 2004). Our study does not favor one of these hypotheses. However, the third hypothesis is unlikely since the juvenile mortality obtained in our study was low (Z = 4.6 yr^{-1}).

Clam density (320 ind. m^{-2}) and biomass (24.2 g SFDW. m^{-2}) in our cage experiment were about twice as high as in the field, at Ile aux Oiseaux and Andernos. However, they probably had little influence on Manila clam growth, as the cage densities were still lower than those found in many natural populations elsewhere. Also, a previous growth experiment at different clam densities failed to demonstrate an effect of clam abundance on growth between biomass ranging from 6.7 to 60.1 g SFDW .m^{-2} (Dang, unpublished data). In Tokyo Bay, before the decline of clams at the end of the 1990s, population density was consistently above 400 ind. m^{-2} (Toba, 2004). Ponurovskii and Selin (1988) reported a population density from 490 to 896 ind. m^{-2} in Vostok Bay and Breber (2002) found 384 ind. m^{-2} of *R. philippinarum* in Goro lagoon. Unpublished data from the Morbihan Gulf showed adult (> 26 mm) densities between 40 and 69 ind. m^{-2} whereas it was between 28 ind. m^{-2} (Ile aux Oiseaux) and 33 ind. m^{-2} (Andernos) in Arcachon Bay. Consequently, abundance of juvenile and adult clams in Arcachon Bay was lower than that of Manila clam populations in many other investigated sites.

To explain the lack of adults > 40 mm, two hypotheses have been envisaged: large clams were collected by fishermen or clams were not able to exceed 40-mm shell-length. Given that asymptotic length was not larger than 44 mm inside the bay and also that fishermen exploit all large size classes, both hypotheses are acceptable. One solution to maintain clam populations would have been that Manila clams in Arcachon Bay compensated for low recruitment by fast growth and low mortality. The necessary time to reach 40-mm shell length depended on the site (Table 1). For instance, clams situated inside the bay required between three and sometimes more than ten yrs to reach 40-mm shell length. At Ile aux Oiseaux (cages 1, 3, 4) and Andernos (cages 3, 4), 40-mm shell length could not be attained. When considering the catch size tolerated in Arcachon Bay, *i.e.* 35 mm, clams from every site can reach this length. The minimum time was 1.6 yrs at Andernos 2 and 1.7 yrs at Arguin 1 whereas it took 4.4 yrs at Gujan 3 (Table 1). The mean age to reach 35 mm was 2.9 yrs, with a minimum of 1.6 yrs at Andernos 2 and 4.4 yrs at Gujan 3. The growth performance index Φ' varied neither between sites nor between elevations above CD. K values in Arcachon Bay (0.3 – 1.21 yr^{-1}) were relatively high compared to other sites such as British Columbia where they varied between 0.14 and 0.39 yr^{-1} (Bourne, 1982). It can be partly interpreted by L_∞ that was dramatically low (< 45 mm in inner lagoon) compared to what was observed in Canada (47.6 – 84.5 mm) (Bourne, 1982). However, low values of L_∞ in Arcachon Bay were not unique and are found in native areas such as in Japanese waters (34.9 mm) (Ohba, 1959).

The present study showed that growth efficiency (K and L_∞) was surprisingly independent of the elevation above CD and that L_∞ alone was different between sites. Influence of elevation above CD on growth has been demonstrated in many suspension feeders like cockles *Cerastoderma edule* in Arcachon Bay (de Montaudouin, 1996). A higher immersion time

corresponds to a higher suspension feeding time (de Kergariou et al., 1981; Goulletquer et al., 1987) and consequently should induce high growth performances. However, Nakamura et al. (2002) and Masu et al. (2008) reported no difference in Manila clam shell length in Tokyo Bay between intertidal and subtidal stations. Bacher and Goulletquer (1989) reported that in intertidal areas, immersion time was an important factor in growth control, but even if this parameter interacted with growth performances, it was not the principal factor explaining the observed differences between sites. Similar observations have been made in a study by Masu et al. (2008) on Manila clam juveniles: shell growth was not exclusively determined by emersion and immersion but perhaps by metabolic rhythm as a result of collective effects of various environmental factors associated with tidal movements, as well as with shell valve movements. Clam growth is also influenced by food supply and water temperature (Thompson, 1984). In Tokyo Bay, Chew (1989) postulated that the growth of Manila clam was affected by temperature, salinity, exposure regime and food availability whereas Nakamura et al. (2002) showed that it could only be explained by food availability. Periods of high growth in *R. philippinarum* were associated with high temperatures, high chlorophyll, lipids and proteins concentrations in water column whereas periods of low growth were related to low temperatures, high turbidity and a high detritic food content in the water (Bacher and Goulletquer, 1989). Differences in asymptotic length between sites may be explained by a varied quality and quantity of trophic sources. The highest L_∞ of this study was found at Arguin. Oceanic sites are commonly characterized by better growth performances because of higher stability of environmental parameters (salinity, temperature) (Mann, 1979; Bacher and Goulletquer, 1989; Robert et al., 1993) and higher trophic supply (Bacher and Goulletquer, 1989; Robert et al., 1993).

The mortality coefficient Z was assessed in cages and *in situ* for two length-classes, < 20 mm (juveniles) and > 20 mm (adults). In cages, average Z was 0.67 yr^{-1} (= 50 % mortality in 12 mo) for juveniles. In both monitored sites (Andernos and Ile aux Oiseaux), juvenile mortality (Z) was 4 - 5 times higher than in cages located in the same site. This difference may result in lower predation in cages and in the fact that juveniles in cages were larger (> 6 mm) at the experiment start than individuals sampled with a 1-mm mesh size (monitoring). Two cages displayed particularly high mortalities for adult clams, due to predation by the oyster drill *Ocenebra erinacea* (Z = 2.3 - 2.6 yr^{-1}) as observed in indications from empty shells. In other cages, average Z was 0.51 yr^{-1} (= 50% mortality in 16 mo). In both monitored sites, (Andernos 4 and Ile aux Oiseaux 2), adult mortality (Z) was 3 - 4 times higher *in situ* than in cages. This difference could result in fishing activity around the cages.

The stock of *R. philippinarum* in Arcachon Bay considerably decreased from 2003 to 2008 and this study highlights the alarming situation of Manila clam populations in Arcachon Bay, as a result of a poor recruitment, slow growth and high fishing effort. The annual production was < 9 g SFDW m^{-2} yr^{-1} compared to 17 g SFDW m^{-2} yr^{-1} in British waters (Humphreys et al., 2007). Furthermore, the productivity in Arcachon Bay was low with a population renewal of around 0.44 yr^{-1} and 0.87 yr^{-1} (average of P/B in 2006 and 2007) at Andernos and Ile aux Oiseaux, respectively. These values were comparable to those of cockles *Cerastoderma edule* from the Wadden Sea which were comprised between 0.46 yr^{-1} and 0.66 yr^{-1} (Ramon, 2003). They were also in the range of the venerid bivalve *Callista chione* with 0.45 yr^{-1} (Metaxatos 2004). A low P/B indicates a low capacity to survive to overexploitation because P/B is considered as an indicator of the maximum limit of sustainable exploitation of stock (Metaxatos, 2004).

In recent years in Japan, at Tokyo Bay and Ariake Bay, the adult stock of Manila clam has drastically decreased, coincident with poor juvenile recruitment (Ishii et al., 2001; Toba, 2004). *R. philippinarum* recruitment occurred twice a year in Tokyo Bay and the decline of the adult stock was associated with the unstable recruitment of summer cohorts, which was the major component of recruitment in the past (Toba et al., 2007).

The possibility of a sustainable population of the Manila clam within Arcachon Bay with such low growth and recruitment is doubtful. Consequently, the survival of Manila clam populations with current levels of extensive fishing activity is unlikely unless high and successful recruitment events occur.

Acknowledgements

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Tables

Table 1.

Growth (K, L_∞, Φ'), environmental parameters (tidal level, immersion time, sediment median grain-size, sediment silt, sediment organic matter), time to reach 35 and 40 mm, and natural mortality Z for clam shell length 4–20 mm (Z_1) and 20–40 mm (Z_2) with determination coefficient (R^2) for the 20 sampling sites in Arcachon Bay.

Sites	K (yr^{-1})	L_∞ (mm)	Φ'	Tidal level (m)	Immersion (% of time)	Sediment median (μm)	Sediment silt (%)	Sediment organic matter (%)	Time to reach 35 mm (yr)	Time to reach 40 mm (yr)	Z_1 (yr^{-1})–(R^2)	Z_2 (yr^{-1})–(R^2)
Arguin 1	0.88	45.89	3.27	1.57	75.00	360	3.5	1	1.7	2.4		
Arguin 2	0.70	46.70	3.18	1.84	70.83	360	3.5	1	2	2.8	0.27 (0.87)	0.42 (0.97)
Arguin 3	0.55	46.90	3.08	2.07	64.58	360	3.5	1	2.5	3.6	0.40 (0.90)	0.22 (0.94
Arguin 4	0.39	43.70	2.87	2.89	37.50	360	3.5	1	4.2	6.5	0.66 (0.88)	0.11 (0.97)
Ile aux Oiseaux 1	1.04	38.14	3.18	1.05	93.75	118	33.25	10.02	2.5		1.03 (0.99)	2.32 (1.00)
Ile aux Oiseaux 2	0.83	40.00	3.12	1.82	52.08	87	43.54	10.32	2.6	>10	0.83 (0.97)	0.51 (0.96)
Ile aux Oiseaux 3	0.92	38.90	3.14	2.03	64.58	76	47.72	10.95	2.6		0.61 (0.96)	2.66 (0.95)
Ile aux Oiseaux 4	0.68	38.20	3.00	2.63	45.14	97	42.45	13.05	3.7		0.61 (0.97)	1.36 (0.97)
Andernos 1	0.44	43.70	2.92	1.18	87.50	118	30.70	9.41	3.7	5.7	0.79 (0.69)	1.11 (0.99)
Andernos 2	1.21	41.30	3.31	1.72	72.92	70	47.88	9.15	1.6	3	1.10 (0.93)	0.45 (0.84)
Andernos 3	0.96	39.50	3.18	1.83	68.75	48	67.96	10.96	2.3		1.22 (0.92)	0.33 (0.77)
Andernos 4	0.97	39.45	3.18	2.11	60.42	163	14.54	3.33	2.3			
Lanton 1	0.45	43.60	2.93	0.83	95.83	95	40.73	10.17	3.7	5.7	0.35 (0.9)	0.75 (0.95)
Lanton 2	0.58	44.60	3.06	1.36	81.94	111	32.19	9.68	2.7	4	0.30 (0.86	0.22 (0.99)
Lanton 3	0.51	42.10	2.96	1.89	70.83	78	40.99	10.09	3.6	6	0.47 (1.00)	0.52 (1.00)
Lanton 4	0.49	43.90	2.98	1.91	65.97	94	36.38	8.49	3.3	5	0.23 (0.91)	0.35 (0.93)
Gujan 1	0.88	41.20	3.17	0.90	95.83	144	23.09	2.52	2.2	4.2	0.61 (0.98)	0.25 (1.00)
Gujan 2	0.52	42.40	2.97	1.46	75.00	69	47.17	5.63	3.4	5.7	0.68 (0.92)	0.27 (0.95)
Gujan 3	0.43	41.60	2.87	1.68	66.67	63	53.13	5.58	4.4	7.8	1.16 (0.95)	0.80 (0.94)
Gujan 4	0.57	40.10	2.96	2.21	56.25	58	54.48	6.13	3.7	>10		

Table 2.
Annual mean biomass, annual mean density, mean body size, somatic annual production and P/B ratio calculated from the size frequency distribution, according to Brey's method, in Andernos and Ile aux Oiseaux for 2006 and 2007. B, biomass. DW, dry weight. P, production.

Site	B (g DW/m^2)	Mean density (clam/m^2)	Mean body size (g DW)	Somatic P (g m^{-2} yr^{-1})	P/B (yr^{-1})
Andernos 2006	9.30	41.8	0.22	4.07	0.44
Andernos 2007	10.11	44.49	0.23	4.56	0.45
Ile aux Oiseaux 2006	5.76	63.64	0.09	5.28	0.92
Ile aux Oiseaux 2007	10.54	120.93	0.09	8.66	0.82

Table 3.
Number and periods of spawning events following the geographic location.

Country	Location	Number of spawning events	Periods	Reference
France	Arcachon Bay	1	Autumn	Robert et al. (1993)
	Ile Tudy (south Brittany)	2	April to August Late summer	Beninger and Lucas (1984)
	Morbihan Gulf	3	June July September	Laruelle et al. (1994)
	Bay of Brest	3	May June September	Laruelle et al. (1994)
	Thau Lagoon	1	April to September	Maitre-Allain (1985)
Spain	Ria de Vigo	2	June to November	Rodriguez-Moscoso et al. (1992)
Italy	Lagoon of Venice	1	May to September	Meneghetti et al. (2004)
Japan	Musaka shoal	2	Late spring Early to late fall	Ohba (1959)
	Tokyo Bay	2	Spring to early summer	Ishii et al. (2001)
	Ariake Sound		Fall to early winter	
	Tokyo Bay (Sanbanse and Kisarazu)	2	Summer Autumn	Toba et al. (2007)
	Matsukawa-ura, (north Japan)	2	Late June to early August Late September to early October	Kanazawa and Sato (2007)
Russia	Vostok Bay	1	Summer	Ponurovsky and Yakovlev (1992)
Canada	British Columbia	1	June to autumn	Holland and Chew (1974), Bourne (1982)
USA	Hood Canal, Washington	1	Early June to September	Nosho and Chew (1972)

Figures
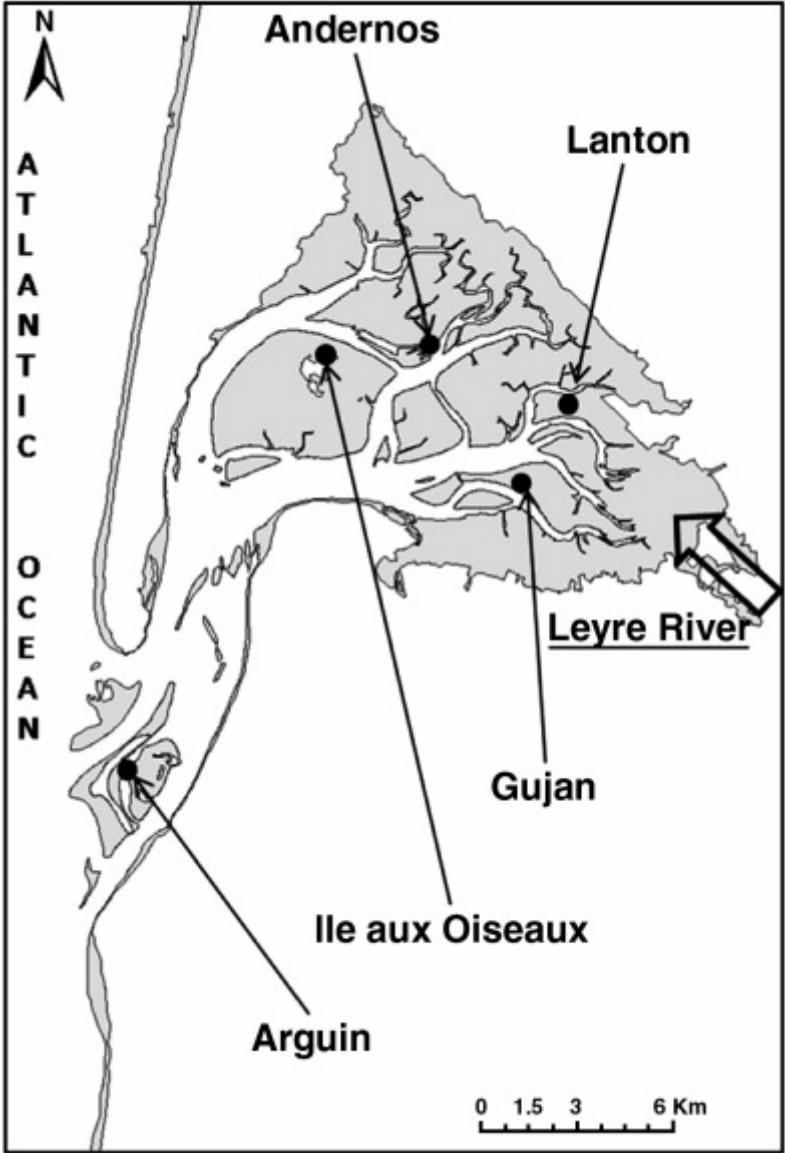
Fig. 1. Position of the five sampling sites Arguin, Andernos, Ile aux Oiseaux, Gujan and Lanton in Arcachon Bay.
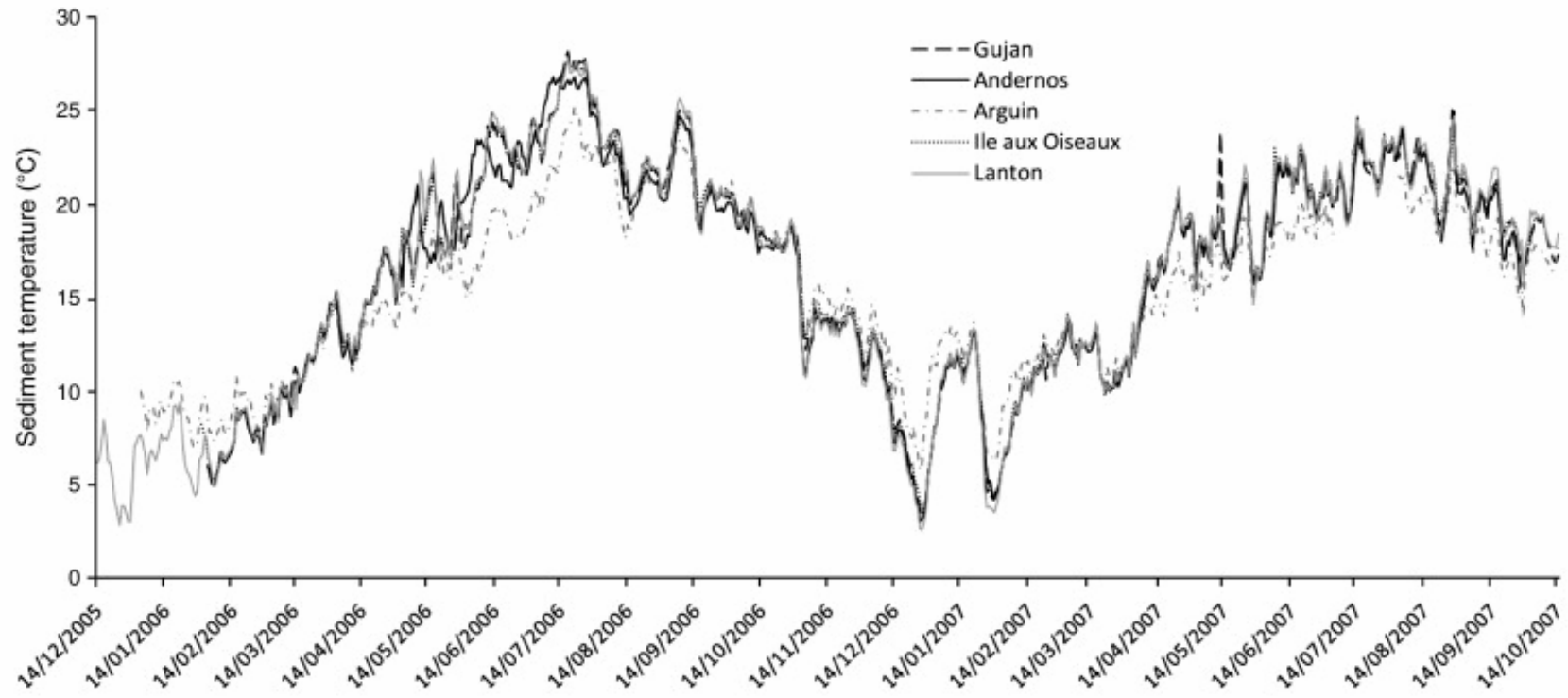
Fig. 2. Mean daily temperatures for the five studied sites from December 2005 to October 2007.
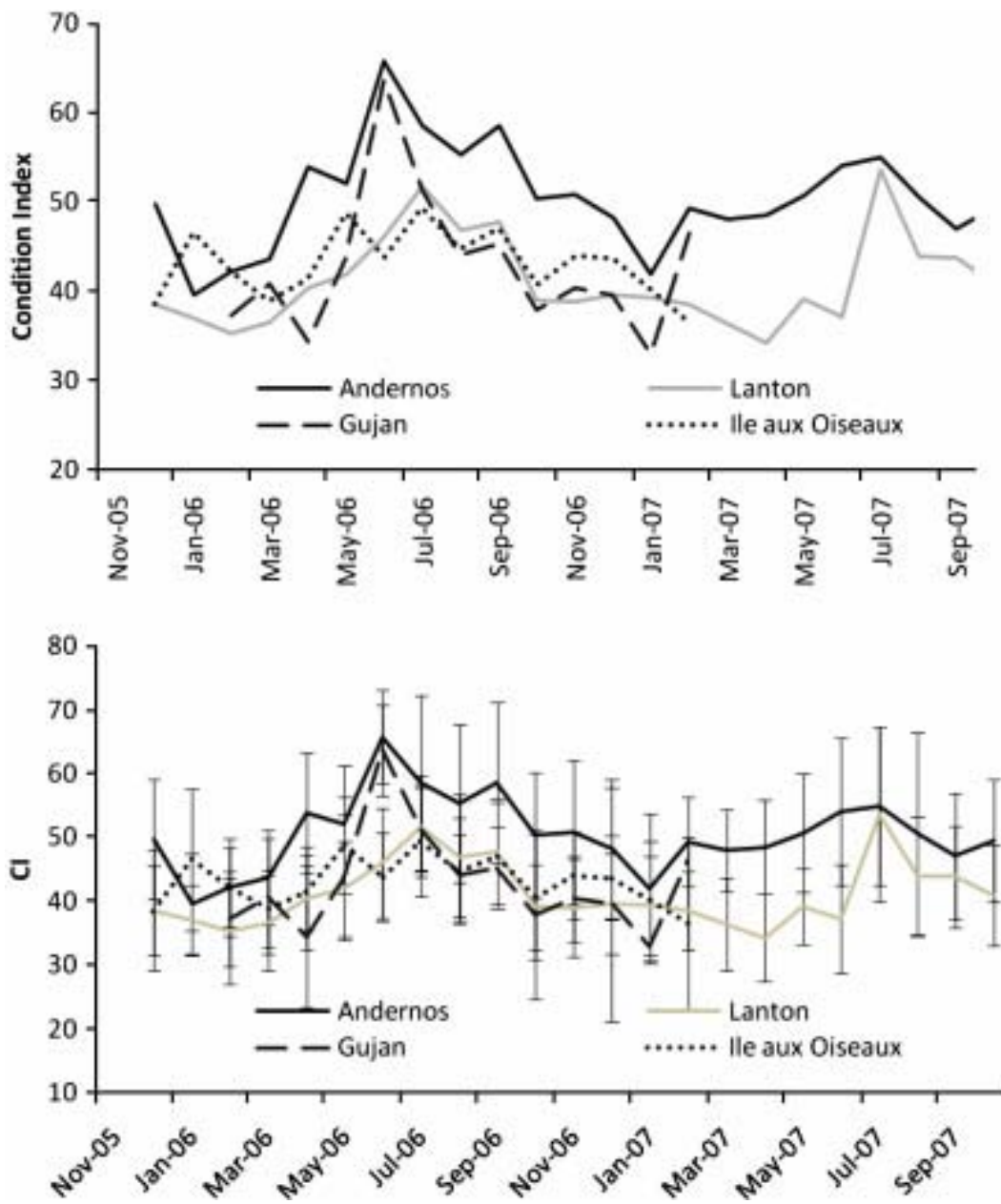
Fig. 3. Mean condition index values of *Ruditapes philippinarum* sampled in Andernos, Lanton, Gujan and Ile aux Oiseaux from December 2005 to October 2007.
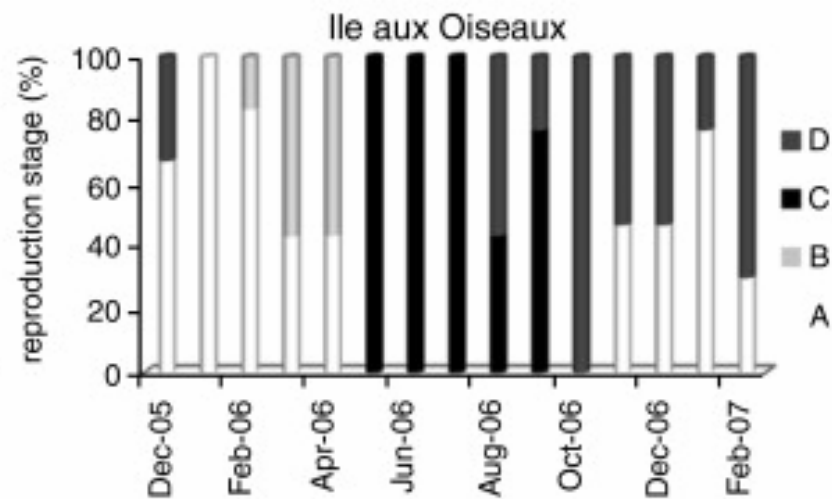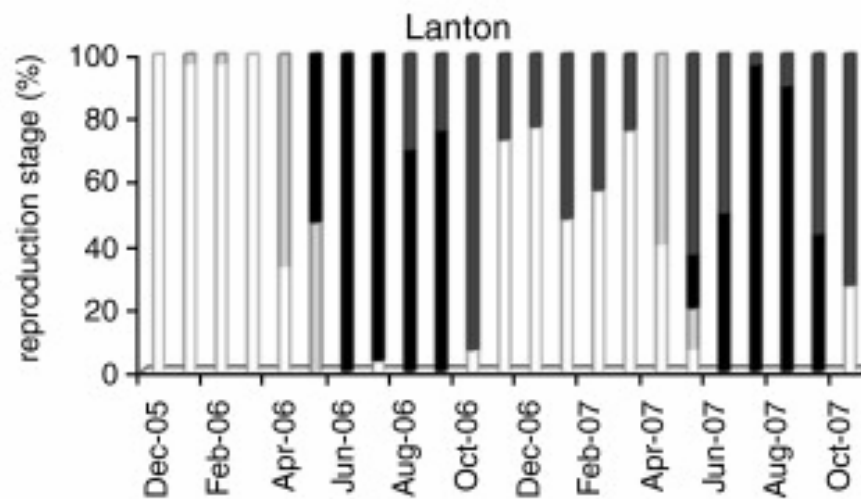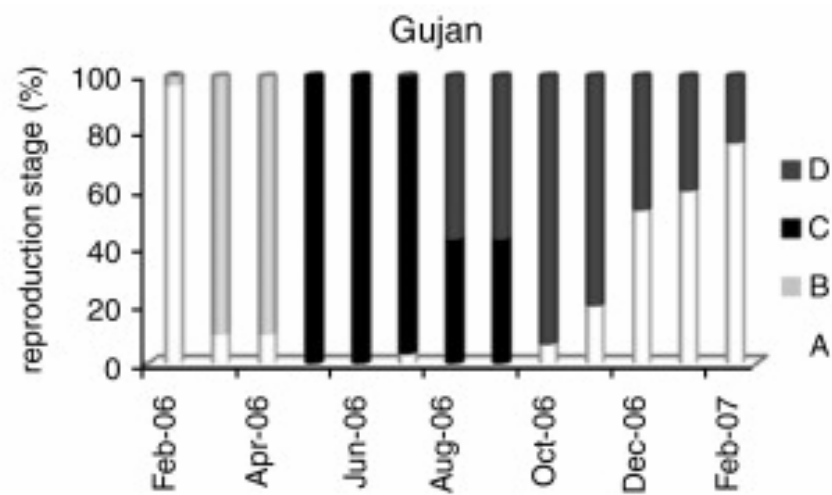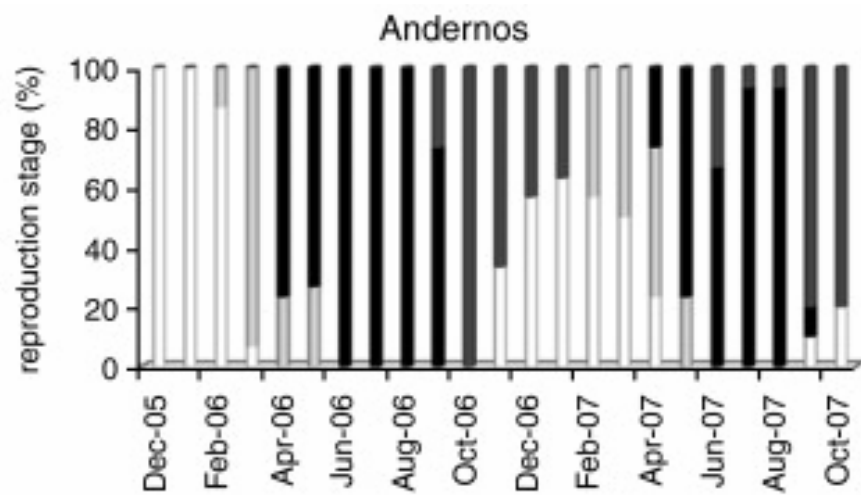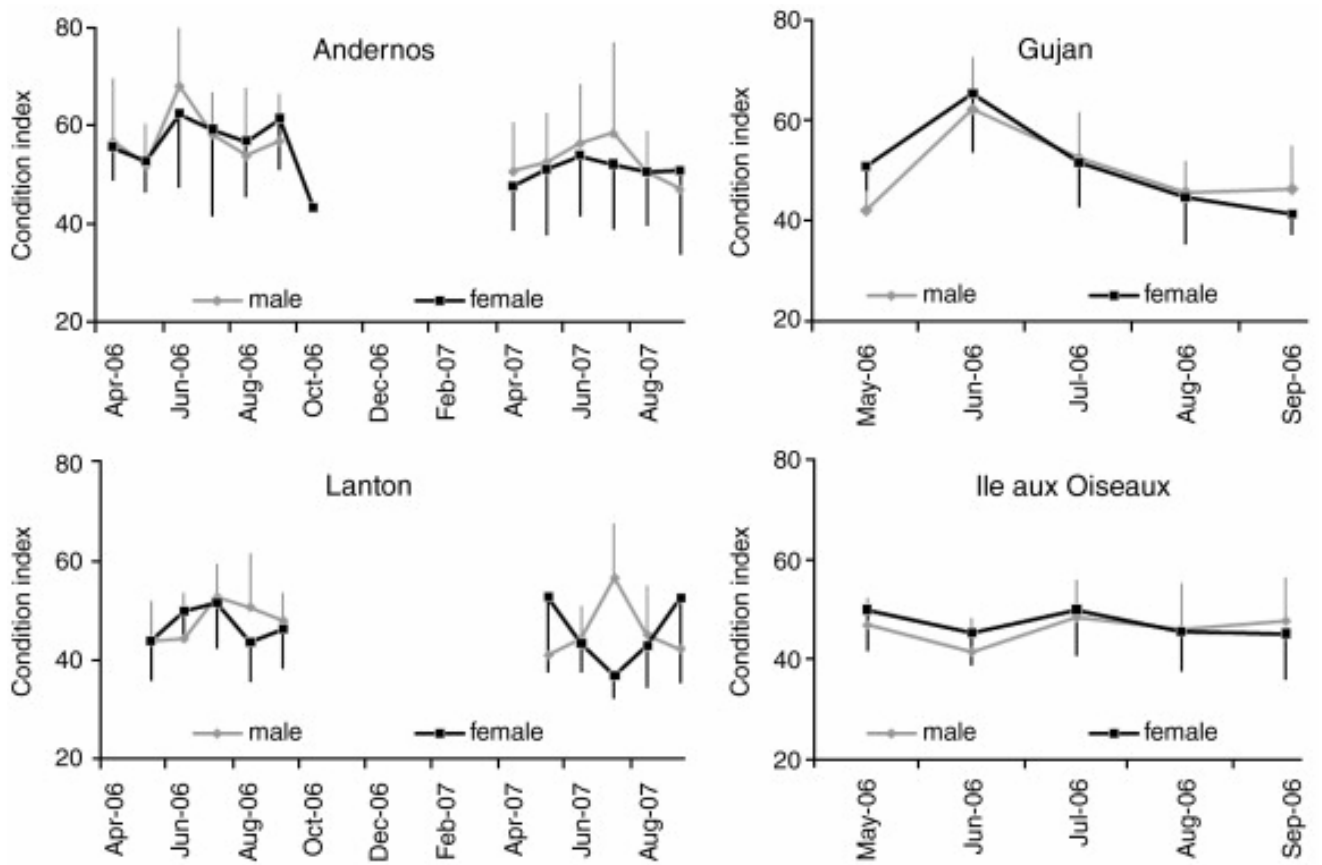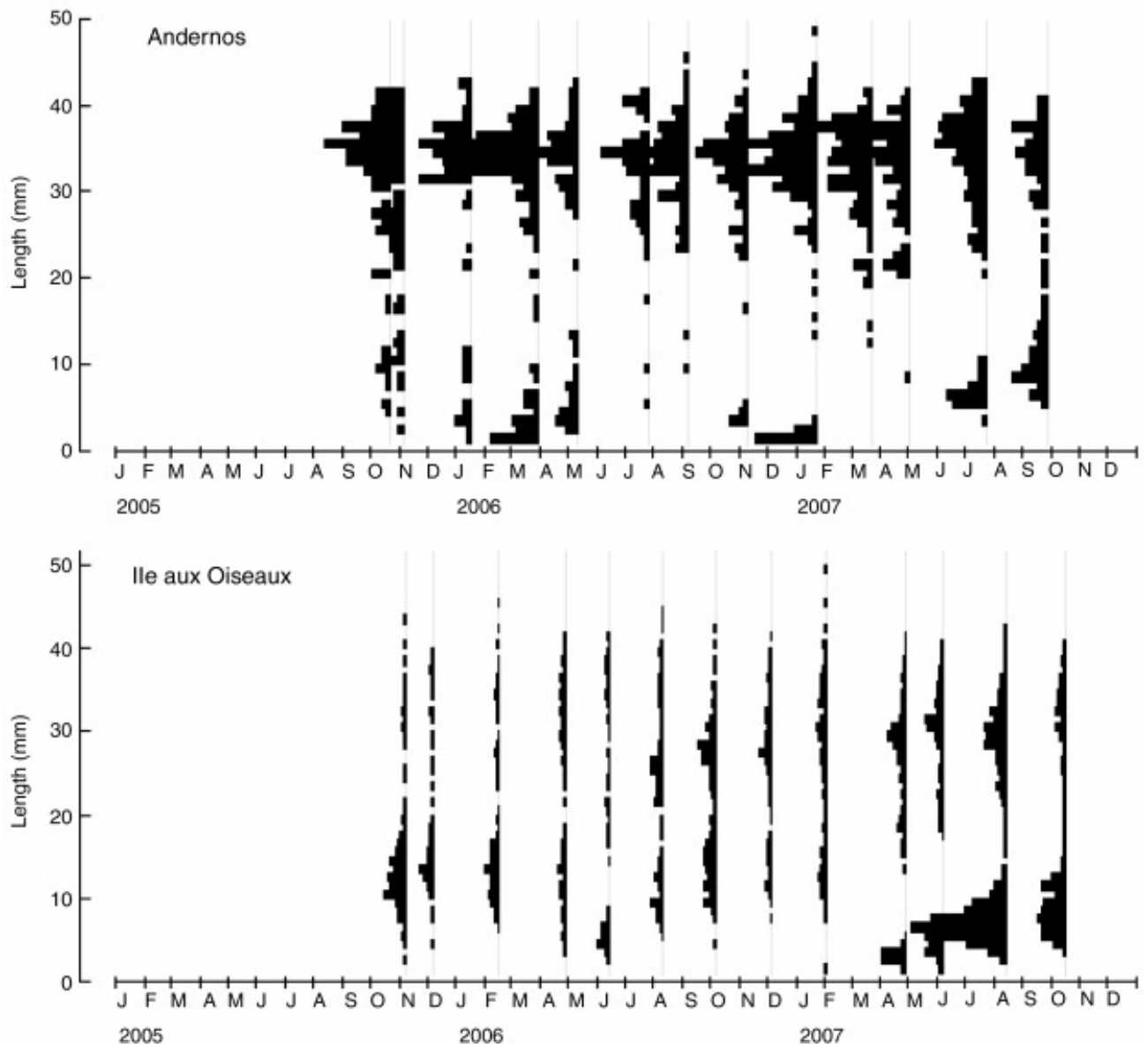
Fig. 4. Reproduction stages (A, B, C and D) of *Ruditapes philippinarum* from December 2005 to October 2007 in Andernos, Lanton, Ile aux Oiseaux and Gujan.

Fig. 5. Condition index (±SD) of *Ruditapes philippinarum* male and female sampled in Andernos, Lanton, Gujan and Ile aux Oiseaux from December 2005 to October 2007.

Fig. 6. Every other month length size frequency distributions of Manila clam *Ruditapes philippinarum* from October 2005 to September 2007 at Andernos and from November 2005 to September 2007 at Ile aux Oiseaux.
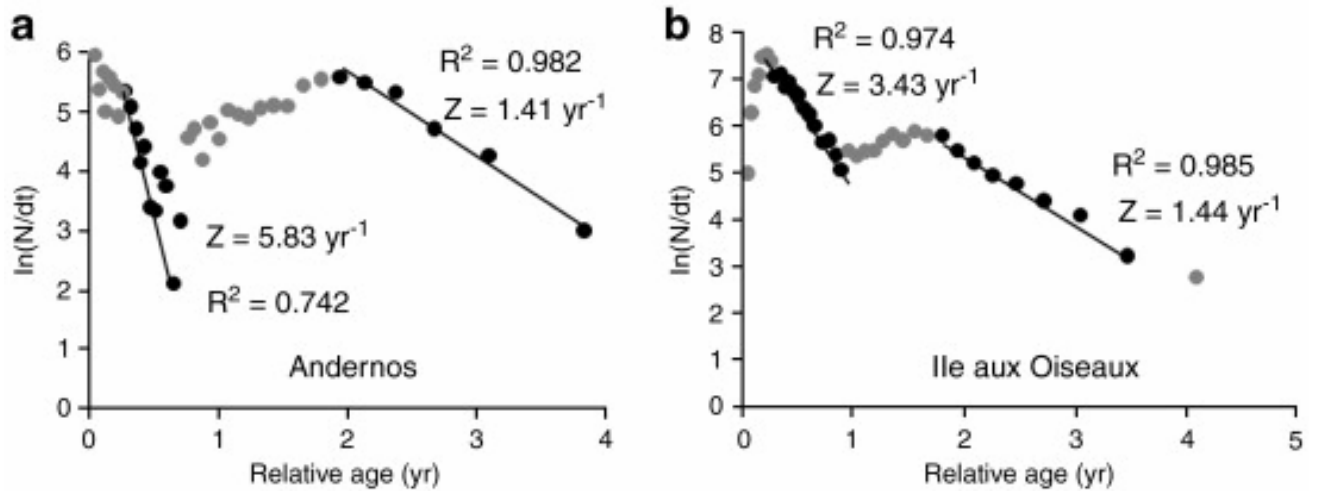
Fig. 7. Size-converted catch curve of *Ruditapes philippinarum* calculated from the size-frequency distribution and the Von Bertalanffy growth curve obtained by FISAT II software following the length catch curve converting method at Andernos and Ile aux Oiseaux.
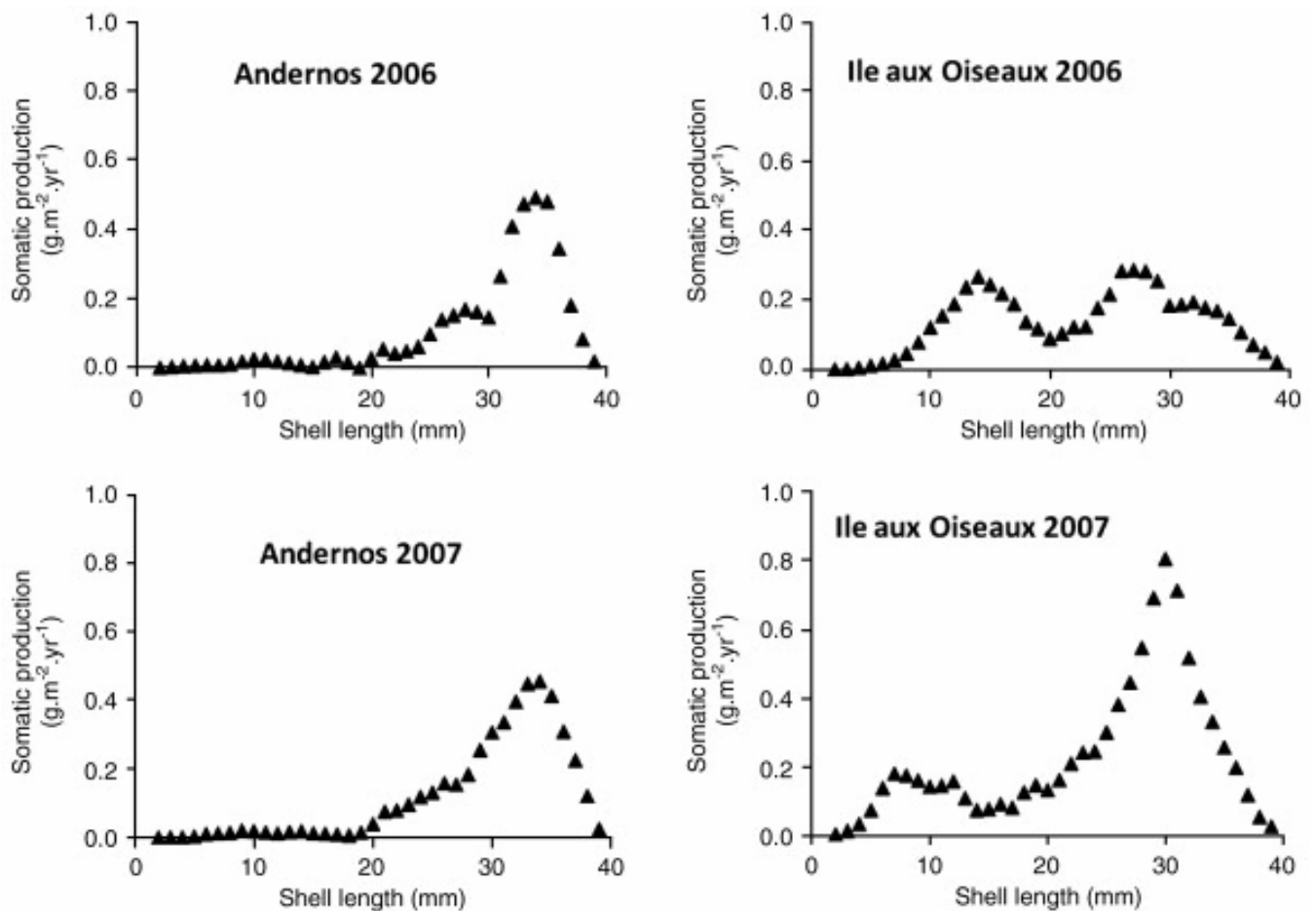

Fig. 8. Somatic annual production (g SFDW.m^{-2}.yr^{-1}) of *Ruditapes philippinarum* per size classes in 2006 and 2007 at Andernos and Ile aux Oiseaux.