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Effects of short-term environmental disturbances on living benthic foraminifera during the Pacific oyster summer mortality in the Marennes-Oléron Bay (France)

Vincent M.P. Bouchet^{1,2}, Jean-Pierre Debenay^{3,2}, Pierre-Guy Sauriau¹, Joël Radford-Knoery⁴,
Patrick Soletchnik⁵

¹ CRELA (UMR 6217 CNRS-IFREMER-ULR), Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, Place du Séminaire, B.P. 5, 17137, L'Houmeau, France

² Laboratoire BIAF (UPRES EA 2644 Université d'Angers), Laboratoire d'étude des bio-indicateurs actuels et fossiles, 2 Bd Lavoisier, 49045, Angers cedex, France

³ IRD, UR Paleotropique, Centre de Nouméa, BP A5, 98848, Nouméa cedex, New Caledonia

⁴ IFREMER, Centre de Nantes, Département Biogéochimie et Ecotoxicologie, B.P. 21105, 44311, Nantes, France

⁵ IFREMER, Laboratoire Environnement et Ressources Poitou-Charentes (LERPC), B.P. 133, 17390, La Tremblade, France

Corresponding author: Bouchet Vincent

E-mail address: vincent.bouchet@ifremer.fr

Telephone: +33(0)5 46 50 06 49

Fax: +33(0)5 46 50 06 00

Abstract

Sediment cores were collected from April to August 2004 on tidal mudflats of the macrotidal Marennes-Oléron Bay (SW France), famous for the cultivation of Pacific oysters (*Crassostrea gigas*). The response of living (stained) benthic foraminifera to short-term biogeochemical disturbances in the sediment and overlying water, which may be involved in oyster summer mortality, was monitored. Short-term hypoxia occurred in early June, in conjunction with a sudden rise in temperature. In mid-June, the ammonia content of sediment porewater increased, leading to potentially maximal flux towards overlying waters. Foraminiferal assemblages, particularly in the topmost layer, were altered. *Ammonia tepida* was the most tolerant to temperature increase and hypoxic conditions whereas *Brizalina variabilis* and *Haynesina germanica* were sensitive to organic degradation and hypoxia. *Criboelphidium gunteri* was the most opportunistic during recolonisation. Benthic foraminifera showed that short-term biochemical changes in the sediment are toxic and may be involved in the summer mortality of Pacific oysters.

Keywords

Living benthic foraminifera – organic matter – hypoxia – ammonium – intertidal – *Crassostrea gigas* – aquaculture – Marennes-Oléron Bay

1. Introduction

In many parts of the world, including Japan, North America and North-western Europe, mass mortality affects the Pacific oyster *Crassostrea gigas* (Thunberg) (Imai, Numachi, Oizumi & Sato, 1965; Glude, 1974; Maurer, Comps & His, 1986; Soletchnik, Le Moine, Faury, Razet, Geairon & Gouletquer, 1999; Cheney, MacDonald & Elston, 2000). Along the French coasts of the Atlantic and English Channel, summer mortality was first reported from the Arcachon Bay during the early 1980s (Maurer et al., 1986), and since then from most shellfish production areas (Costil, Royer, Ropert, Soletchnik & Mathieu, 2005; Dégremont, Bedier, Soletchnik, Ropert, Huvet, Moal et al., 2005; Soletchnik, Lambert & Costil, 2005). A number of studies have established that summer mortality not only occurs during periods of physiological stress associated with gonad development and maturation, but it is also driven by complex interactions between environmental factors and oyster-farming practices. For example, in Marennes-Oléron Bay, daily mortality rates of “on-bottom” oysters, reared directly on the intertidal sediments, were significantly higher than those of “off-bottom” oysters reared on trestles (Soletchnik et al., 1999; Soletchnik et al., 2005; Gagnaire, Soletchnik, Madec, Geairon, Le Moine & Renault, 2006). These observations provide circumstantial support for the idea that intertidal muddy sediments play a role in the summer mortality of Pacific oysters (Soletchnik et al., 1999; Soletchnik et al., 2005; Gagnaire et al., 2006). As reported for blue mussel farming (e.g. Grant, Hatcher, Scott, Pocklington, Schafer & Winters, 1995; Ragnarsson & Raffaelli, 1999; Christensen, Glud, Dalsgaard & Gillespie, 2003; Hartstein & Rowden, 2004), the properties of soft-sediments beneath oyster cultivation sites are modified by significant organic enrichment due to biodeposition of faeces and pseudofaeces, and sedimentation of silt (Sornin, Feuillet, Héral & Deslous-Paoli, 1983; Nugues, Kaiser, Spencer & Edwards, 1996; Mallet, Carver & Landry, 2006). Driven by seasonal and tidal cycles, simultaneous increase in temperature, availability of organic

biodeposits, and varying oxidation levels in the surface sediment can lead to active mineralisation of sedimentary organic matter. This phenomenon favours geochemical cycling within the sediments, with a complex balance between aerobic and anaerobic processes (Sornin et al., 1983; Lerat, Boucher & Le Corre, 1985; Feuillet-Girard, Héral, Sornin, Deslous-Paoli, Robert, Mornet et al., 1988; Santschi, Höhener, Benoit & Buchholtz-ten Brink, 1990). On some occasions, back-diffusion of released toxic nutrients such as ammonia and sulphur to the water column may occur (Sornin et al., 1983; Feuillet-Girard et al., 1988; Santschi et al., 1990; Vouvé, Guiraud, Marol, Girard, Richard & Laima, 2000; Gray, Wu & Or, 2002). Physicochemical and geochemical changes resulting from the input of organic deposits associated with oyster cultivation influence benthic communities and can modify species richness and distribution patterns of soft-bottom macrofauna (Castel, Labourg, Escaravage, Auby & Garcia, 1989; Nugues et al., 1996; Deslous-Paoli, Souchu, Mazouni, Juge & Dagault, 1998) and meiofauna (Castel et al., 1989; Dinét, Sornin, Sablière, Delmas & Feuillet-Girard, 1990). Although benthic foraminifera have been used successfully as biological indicators to assess the status of various pristine or polluted ecosystems (Alve, 1995a, b; Grant et al., 1995; De Rijk, Jorissen, Rohling & Troelstra, 2000; Annin, 2001; Debenay, Tsakiridis, Soulard & Grosseil, 2001; Alve, 2003; Morvan, Le Cadre, Jorissen & Debenay, 2004; Debenay, Bicchi, Goubert & Armynot du Châtelet, 2006), only a few studies have been carried out on benthic foraminifera related specifically to aquaculture. The main ones are those carried out in Atlantic Canada by Schafer, Winters, Scott, Pocklington, Cole & Honig (1995) and Scott, Schafer, Honig & Younger (1995), related to blue mussel and salmon aquaculture respectively, and in the Red Sea by Angel, Verghese, Lee, Saleh, Zuber, Lindell et al. (2000), which was related to fish farming. As far as we know, temporal variations of benthic foraminiferal assemblages associated with oyster cultivation have never been described. It is well established that foraminifera responses, such as changes in species richness, dominance of calcareous vs. agglutinated species, specific depth distribution and test

morphology, are related to environmental parameters. Among the factors reported to affect foraminiferal assemblages, both oxygen availability and organic matter fluxes are regarded as major structuring forces acting on benthic foraminifera in marine environments (van der Zwaan, Duijnste, den Dulk, Ernst, Jannink & Kouwenhoven, 1999; De Rijk et al., 2000; den Dulk, Reichart, van Heyst, Zachariasse & van der Zwaan, 2000; Ernst, Bours, Duijnste & van der Zwaan, 2005).

In the present study, changes in living (stained) benthic foraminiferal assemblages were analysed and compared with temporal changes in the properties of intertidal sediments influenced by Pacific oyster cultivation during a critical period in spring/summer oyster mortality. The parameters taken into account were the concentration in sedimentary organic matter, dissolved ammonia and sulfide dynamics within the sediment porewaters and the hydrology (temperature, salinity, turbidity and oxygen saturation) of the overlying waters. The aim of the study was to use the rapid response of foraminiferal assemblages to environmental parameters in order to assess the impact of physiochemical changes on benthic communities.

2. Materials and methods

2.1. Site location and survey design

The study was carried out at Ronce-Perquis, an intertidal oyster cultivation area located in the southern part of Marennes-Oléron Bay, on the French Atlantic coast north of the Gironde estuary (Fig. 1). Experiments were performed in an oyster park subject to 50-65% immersion, i.e. emergent at low tide when the tidal coefficient is over 60-70. Tidal coefficients range from 20 to 120 according to SHOM (Service Hydrographique de la Marine, Brest), corresponding to extreme neap tides and extreme spring tides, respectively. Pacific oysters *Crassostrea gigas* were reared in plastic mesh bags placed on trestles at 70 and 15 cm above

the sediment surface, hereafter called “off-bottom” and “on-bottom” culture, respectively. The initial rearing density was set at 200 oysters per bag, and mortality rates were estimated by counting dead and live specimens at each sampling date.

Soletchnik et al. (1999), in their study on dynamics of oyster mortality at the same site, reported that the oyster mortalities are seasonal, occurring during spring and summer. The period selected for the study of temporal variations in water column parameters, sediment properties and foraminiferal assemblages was chosen on the basis of this previous study. Samples were collected between 22 April (before the beginning of oyster mortality) and 4 August 2004 (several weeks after the mid-June, mortality maximum). Sediments were analysed on 22 April, 6 and 25 May, 9, 14, 22 and 30 June and 4 August, and foraminiferal assemblages collected on 22 April, 25 May, 9 and 22 June, and 4 August.

Figure 1

2.2. Bottom water characteristics

A YSI multiparameter probe was deployed 15 cm above the sediment surface of the oyster cultivation site. The YSI probe measured temperature, salinity, oxygen content and turbidity (measured in Nephelometric Turbidity Units, NTU) continuously for 2 min every 15 min from April to August 2004.

2.3. Sediment temperature and biochemistry

Two temperature loggers (StowAway TidbiT, ONSET) were deployed at the water-sediment interface and at 15 cm sediment depth. Both were set to measure temperature every 10 min for the entire study period. Furthermore, on each sampling date, in situ sediment temperature, pH and redox levels were determined using a Cyberscan pH 300 series probe (EUTECH Instruments) at 1 and 4 cm below the water-sediment surface of sediment cores sampled at

low tide. Measurements were made immediately through 1 cm-spaced holes predrilled into the core tube.

For organic matter analyses, the top of two sediment cores (diameter = 73 mm) was sliced off in two layers (0-1 cm and 1-2 cm) and each one homogenized. One sub-sample of sediment organic matter (SOM) was analysed for particulate organic carbon and nitrogen (POC and PON) using a C/N analyser (Carlo Erba NA 1500), and carbon and nitrogen stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) following procedures described by Riera, Richard, Grémare & Blanchard (1996). Carbon and nitrogen stable isotopes were analysed using a mass spectrometer (Micromass, Manchester, UK) interfaced to an elemental analyser EuroEA3024-IRMS (Eurovector, Milan, Italy). Data were expressed in the standard δ notation as parts per thousand (‰) relative to the Peedee Belemnite Limestone (PDB) and atmospheric N_2 for carbon and nitrogen, respectively. Replicate analyses of SOM show a standard deviation of 0.1 ‰ for both C and N isotope ratios, which was small, compared to between-sample variability (Bouchet & Sauriau, unpub. data). The top 1 cm sediment chlorophyll *a* (chl *a*) and phaeopigment concentrations were determined following Lorenzen's method (Holm-Hansen, Lorenzen, Holmes & Strickland, 1965). Two subsamples were freeze-dried, extracted overnight in 90% acetone (4°C), centrifuged 10 min at 2000 rpm, analyzed spectrophotometrically (Turner 10 AU), and corrected for phaeopigments, which were determined after 1N HCl treatment (Yentsch & Menzel, 1963).

For dissolved ammonia (NH_4^+ and NH_3) and sulfide (H_2S) analyses in pore water, 73 mm diameter transparent acrylic tubes, were used to retrieve 20 cm long sediment cores.

Immediately after sample collection, porewater extraction began. Predilled 1 cm-spaced holes in the core tube covered with electrical tape allowed easy insertion of glass-fibre reinforced Rhizon in situ samplers (RISS, described in Seeberg-Elverfeldt, Schlüter, Feseker & Kölling, 2005). A maximum of 2 ml of porewater (0.1 μm -filtered by the RISS) was then vacuum

extracted at each sampling depth using 2.5 ml polyethylene syringes tipped with Luer-Lock 3-way valves. Once the extraction was complete (10 to 30 min.), the syringes were then used to dispense the appropriate amount of sample into polyethylene test tubes and analyses carried out immediately. The RISS devices are particularly convenient because the entire sample collection process is conducted without atmospheric contact and hence adverse effects on sulfide or ammonia oxidation. Commercially available reagents (Merck Ammonium ref 1.14752 and Merck Sulfide ref 1.14779) were used to determine sulfide and ammonia. The methods are based the well-known methylene blue (e.g., Cline, 1969) and indophenol reactions (e.g., Solorzano, 1969). The amounts of the reagents used for each analysis were scaled to the sample volume. External calibrations were carried out using an aqueous matrix identical to that of the sample but ammonium- and sulfide-free in order to avoid for any potential interference in the chemical reactions involved. Sulfide determinations were performed on undiluted porewaters, whereas ammonia samples were diluted with ultrapure water 5- to 20-fold before analysis. Reported concentrations are well above the detection limits, and precision is estimated to be 10% or better, based on replicate analyses and on the calibration using linear, least squares regression fits.

2.4. Samples for benthic foraminifera

At each sampling date, the superficial sediment (0-0.5 cm) was scraped off over a 1-2 m² surface, using a “pseudoreplication” procedure (Hurbert, 1984) that limits the potential bias due to the patchiness of foraminifera. In addition, one core was collected using a coring tube (8 cm long and 7.5 cm in diameter), capped on site and transported back to the lab for processing. The core was sliced into 5 segments i.e. 0-0.5 cm, 0.5-1 cm, 1-3 cm, 3-5 cm and 5-8 cm in order to describe the vertical distribution of benthic foraminifera. Each sample was preserved in 70% ethanol with 1 g l⁻¹ Rose Bengal for staining foraminifera in order to

distinguish stained (living) from dead specimens (Murray & Bowser, 2000). This study solely focused on living foraminifera as recommended by Murray (2000). After at least three days in the staining solution, samples were washed through 50 μm mesh sieves and dried at 50°C. After drying, tests were concentrated by heavy liquid flotation using carbon tetrachloride (CCl_4). Before examining foraminifera, each sample was split into two aliquots from which two counts were made. When necessary, the aliquots were divided again to give a maximum of approximately 2000 living specimens. These specimens were carefully spread over a picking tray with 42 cells. Cells were selected randomly and all the living specimens in each cell were picked and counted, until a total of at least 150 specimens, under a stereomicroscope (Leica MZ75). Only the living specimens were identified. Fatela & Taborda (2002), in their study on the confidence limits of benthic foraminiferal counts, demonstrated that counts as low as 100 specimens are sufficient in studies based on the species representing at least 5% of the assemblage. For recognition of “living” specimens, opaque agglutinated and porcelaneous tests were completely soaked in the water, over a white bottom, to allow observation of stained cytoplasm to be made. Species were classified according to Loeblich and Tappan’s ordinal classification (1988). Abundances were expressed as total number of living specimens in 50 cm^3 of sediment and abundances of each stained species (number of living individuals in 50 cm^3 of sediment) was determined. The relative abundance of stained foraminifera species within a sediment layer was calculated. The species richness was defined as the number of living (stained) species per 150 individuals within a sediment layer. At each sampling date, 40 living (stained) specimens of *Ammonia tepida* were randomly picked from the first two core layers i.e. 0-0.5 and 0.5-1 cm. The maximum diameter of their tests was measured in order to assess size frequency distributions of the *A. tepida* population.

2.5. Data analysis

Depth profile of ammonia and sulfide concentrations were mapped by kriging methods using Surfer 6 (Golden Software Inc.). Both data sets were fitted with linear variogram models, which incorporated anisotropy to take into account the higher continuity between data points located along the vertical axis.

Distribution patterns of living (stained) foraminifera abundances are represented by using rank-frequency diagrams (RFD). This technique relies on ranked frequencies of species plotted against their respective ranks organized in decreasing order, and with both axes in logarithmic scale (Legendre & Legendre, 1984; Frontier, 1985). Ecological interpretation of RFDs was reviewed by Frontier (1985) in a comparison of mathematical models (Mouillot & Lepretre, 2000). It relies on the recognition of 3 ecological succession stages associated with 3 different RFD curve shapes: linear-concave = pioneer assemblage with low species richness (stage 1); convex = intermediate assemblage with increasing species diversity (stage 2) and straight-line = mature assemblage (stage 3) (Fig. 7d). In some cases, a straight-line may reflect mixtures of different assemblages of intermediate diversity. The method was successfully applied to compare polluted vs. unpolluted macrobenthic assemblages (Hily, 1983) and to describe their long-term changes (e.g. Davoult, Dewarumez & Migné, 1998). For example, ecological succession from pioneer assemblage to mature assemblage reveal a recovery in the assemblage (dotted arrow in Fig. 7d).

Student t-test for paired data was performed to evaluate the null hypothesis that total and specific foraminiferal abundances from surface sediments did not differ between sampling methods (i.e. pseudoreplication vs. core sampling). One-way and two-way ANOVA with replication and fixed effects were performed to test, for instance, the null hypothesis that temporal changes in environmental conditions of the sediments did not affect the abundances and depth distribution of the foraminiferal taxa. Prior to ANOVA analyses, species abundances were square-root transformed in order to improve equality of variances and

normality (Zar, 1984). A Kolmogorov-Smirnov goodness of fit test (K-S test) was used to reveal any differences in size distribution frequencies in the *Ammonia tepida* population between the surface (0-0.5 cm) and the subsurface (0.5-1 cm) sediment layers. All statistical analyses were performed with Statistica v.7.1 or computed according to Zar (1984).

3. Results

3.1. Variations in bottom water characteristics

The salinity of the water over the oyster culture site ranged from 31 to 35 except during 5 days in early May, when values ranged from 25 to 30. Although the turbidity of the bottom waters was lower than 100 NTU most of the time, there were two periods with values higher than 900 NTU, i.e. on 12 May and between 26 May and 10 June (Fig. 2). During this last period, oxygen levels dropped to hypoxic conditions (20% air-saturation) compared to normoxic conditions recorded before 26 May and after 10 June (Fig. 2).

Figure 2

3.2. Variations in sediment temperature and oyster mortality

Mean daily temperature at the sediment water interface increased from 13.3°C in April to 21.9°C in early August (Fig. 3). Increase in temperature was however discontinuous since two periods of sharp increase occurred, one in mid-May (+ 4°C in 6 days) and the other in early June (+4.0°C in 10 days) (Fig. 3). During these two periods, the temperature range was the highest. This led to a difference of ca. +12°C between the minimal and maximal daily temperature in a few days, in conjunction with an increase in the spring tide amplitude. The fact that periods of the highest day-to-day temperature variability coincide with extreme spring tides in Marennes-Oléron Bay results from the occurrence of extreme low spring tide at midday. From 15 June to 4 August, day-to-day variation in mean temperature was reduced and

ranged from 19.2 to 21.9°C (Fig. 3). Variations in temperature at 15 cm depth followed similar trends but were smoother, the daily temperature amplitude being lower than 1.5°C (Fig. 3).

The highest daily mortality rates of oysters were observed from early to mid-June for both rearing conditions after mean temperature had reached 18-19°C on 5 June and day-to-day temperature reached its highest, 28°C on 7 June (Fig. 3). Daily mortality rates were always significantly higher for “on-bottom” than for “off-bottom” rearing conditions (two-way ANOVA results: $P < 0.01$) with maximum mortality rates of 0.43 day⁻¹ (Fig. 3). After a 6-month rearing period, cumulative mortality was also significantly higher for “on-bottom” than for “off-bottom” conditions (Student t test results $P < 0.001$), with cumulative values of 14.8 ± 2.9 and $5.7 \pm 0.9\%$, respectively.

Figure 3

Table 1

3.3. Variations in sediment characteristics

The measures of sediment characteristics are found on Table 1.

Salinities recorded within intertidal sediment porewater ranged from 31 to 35, similar to those of the overlying bottom water. The temperature of surface sediments (at 1 cm depth) was higher than that of subsurface sediment (at 4 cm depth) from June to August when both pH and Eh values were lower in surface than subsurface sediments. Respective ranges of pH and Eh were 6.9 to 8.0 and -112 to -183 mV. For surface sediments, the lowest Eh was recorded on 22 June (-160 mV) and then increased to -112 mV on 4 August.

Chlorophyll *a* contents from the top 1 cm of the sediments continuously increased from early April to 9 June, suddenly dropped on 14 June and then increased again from the end of June to early August. Phaeopigments followed a similar trend with maximal values on 9 June ($> 1500 \pm 700 \text{ mg m}^{-2}$) followed by minimal values ($\text{ca } 300 \pm 60 \text{ mg m}^{-2}$) on 14 June. Chlorophyll *a*

and phaeopigments at 1-2 cm depth were always significantly lower than those of the top 1 cm of sediments (ANOVA results: $P < 0.001$ and $P < 0.01$ respectively) but exhibited similar seasonal changes. Particulate organic carbon (POC) and nitrogen (PON) also matched these seasonal variations with minimal values recorded on 14 June after maximal values on 9 June, whatever the sediment layers. Values of POC and PON recorded at the end of June and early August were similar or higher than those recorded on 9 June. C/N ratios were relatively stable over the sampling period and ranged from 6.6 to 7.5. Similarly, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the top 1 cm of sediments did not exhibit large variations and ranged from -20.5 to -21.8 ‰ and 5.9 to 6.4 ‰, respectively.

Temporal changes in porewater profiles of ammonia and sulfide content within the sediment matrix revealed the occurrence of peak values in mid-June at 5-6 cm depth and in early July at a depth of 0.5 cm, respectively (Figs. 4a, b). Maximum values of porewater ammonia content occurred from 14 to 22 June and extended through the entire sedimentary column on 14 June with a peak value of 45 mg l^{-1} (Fig. 4 a). A similar phenomenon occurred in porewater sulfide content on 30 June with a maximal value of 0.62 mg l^{-1} but this event occurred within a stable background content averaging $0.1\text{-}0.2 \text{ mg l}^{-1}$. It also came after a small peak, which started on 25 May at 1.5 cm and extended up to the sediment-water interface by 14 June (Fig. 4b).

Figure 4

3.4. Living (stained) foraminifera: species richness and abundances

T-tests for paired data were performed to compare the pseudoreplication and core sampling protocols using results from surface sediments. Neither living (stained) foraminiferal species richness nor total and specific abundances of surface sediments varied significantly from one method to the other (Table 2). Patchiness affects the results on one date but its effect is reduced on a long-term series of samples.

Table 2

Thirty living (stained) species were determined (Appendix A). Species richness significantly varied by sampling date and depth (two-way ANOVA results: $P < 0.001$) with maximum and minimum values recorded in surface and deep sediment layers, respectively (Fig. 5). On three dates, 25 May, 9 June and 4 August, species richness at 0.5-1 cm was significantly higher than that at 0-0.5 cm (Fig. 5).

Figure 5

Temporal changes in depth profiles of relative abundances were highly significant (two-way ANOVA results: $P < 0.001$) and the lowest relative abundances of living foraminifera were recorded within the 1–3 to 5-8 cm layers on 22 June. Living specimens were mainly concentrated within the topmost 1 cm of sediments (Fig. 5).

Temporal changes in abundances of living foraminifera were highly significant (two-way ANOVA results: $P < 0.001$) with a decrease by 50 to 65% in living specimens for both the 0-0.5 and 0.5-1 cm layers from early April to 9 June (Fig. 5). The abundance of living foraminifera for surface sediments (0-0.5 cm depth) had recovered by the end of June but that of subsurface sediments (0.5-1 cm depth) did not and remained lower than initial values (Fig. 5).

Benthic foraminiferal assemblages were dominated by 6 species i.e. *Ammonia tepida* (Cushman), *Brizalina striatula* (Cushman), *Criboelphidium excavatum* (Terquem), *Criboelphidium gunteri* (Cole), *Haynesina germanica* (Ehrenberg) and *Quinqueloculina seminula* (Linné) (Appendix A). Four of these species (*Ammonia tepida*, *Brizalina striatula*, *Criboelphidium gunteri* and *Quinqueloculina seminula*) exhibited higher abundances at depths of 0-0.5 cm than at 0.5-1 cm (Figs. 6a, b, d, f, two-way ANOVA results: $P < 0.001$). *Ammonia tepida* was the most abundant and comprised up to 76% of total abundance of stained species (Appendix A). Its abundances significantly decreased from 22 April to 9 June

(Fig. 6a) (two-way ANOVA results: $P < 0.001$) in both 0-0.5 and 0.5-1 cm layers, with 46 and 41% of the total abundance of live specimens, respectively (Appendix A). The decrease of the abundance was however significantly higher within the 0.5-1 cm depth range (two-way ANOVA, results: $P < 0.001$). On 22 June, the abundance of *A. tepida* was again above 7000 specimens per 50 cm^{-3} in surface sediments whereas it was lower than 3000 specimens per 50 cm^{-3} at 0.5-1 cm (Fig. 6a). At the end of the survey, the *A. tepida* abundance was still significantly higher at 0-0.5 cm than at 0.5-1 cm (two-way ANOVA results: $P < 0.001$). *Haynesina germanica* and *Brizalina striatula* were largely represented on 22 April in both the 0-0.5 and 0.5-1 cm layers (Figs. 6b, e) but their abundances significantly declined during the survey (two-way ANOVA results: $P < 0.001$). In contrast, *Criboelphidium excavatum* exhibited significant peaks in density on 25 May in the 0-0.5 cm layer and on 22 June in the 0.5-1 cm layer (two-way ANOVA results: $P < 0.001$). On 22 June, *C. excavatum* was the dominant species in place of *A. tepida* in the 0.5-1 cm layer but its abundance on 4 August was lower than that on 22 April (Fig. 6c). At the end of the survey, *Criboelphidium gunteri* became the second most dominant species after *A. tepida* in the 0-0.5 cm layer with a highly significant increase in density (two-way ANOVA results: $P < 0.001$).

Figure 6

3.5. Structure of living (stained) foraminiferal assemblages

From 22 April to 25 May, rank-frequency diagrams (RFDs) from topmost sediments (0-0.5 and 0.5-1 cm) appeared as a straight line (Figs. 7a, b). On 9 June and 22 June, RFD appeared to be more convex and those of 4 August linear concave. All RFDs of deeper layers (5-8 cm) were convex and characterized by a lower species richness than those of surface sediments (Fig. 7c). From 22 April to 4 August, large changes in RFDs appeared for surface sediments due to changes in species richness and species dominance (Figs. 7a, b, Appendix A). On 22 April, *Ammonia tepida*, *Brizalina striatula* and *Haynesina germanica* dominated foraminiferal

assemblages, composed of 14 species, in the 0-0.5 cm layer, and *A. tepida*, *Criboelphidium excavatum* and *B. striatula* dominated the low-diversity foraminiferal assemblage, made up of only 8 species, in the 0.5-1 cm layer. Several species were absent from surface sediments on 9 June such as *Bolivina pseudoplicata* Heron-Allen & Earland, *Brizalina variabilis* (Williamson), *Fissurina lucida* (Williamson), *Massilina secans* (d'Orbigny), *Adelosina bicornis* (Walter & Jacob), *Qinqueloculina jugosa* Cushman, *Q. seminula* (which was the second most abundant species on 22 June), *Reophax scorpiurus* de Monfort, *Rosalina* cf. *vilardeboana* (d'Orbigny) and *Spirillina vivipara* Ehrenberg (only recorded on 22 April). In contrast, several species were recorded mainly on 9 June in surface sediments, such as *Brizalina spathulata* (Williamson), *Bulimina elegans* d'Orbigny and *Eggerelloides scabrus* (Williamson), the later being recorded earlier in both the 3-5 and the 5-8 cm layers on 22 April (Appendix A).

Foraminiferal assemblages from the 5-8 cm sediment layers were dominated equally by two species i.e. *Ammonia tepida* and *Criboelphidium excavatum*, and this explained the more convex shape of the RFDs (Fig. 7c). The third most abundant species was *C. gunteri*, but on 9 and 22 June, *C. gunteri* was not recorded and was replaced by *Haynesina germanica*. From 22 April to 4 August, no differences in the shape of the RFDs from the 5-8 cm layers were apparent although a higher number of rare species was recorded on 22 April (Fig. 7c). The dominance by species reported on 22 April i.e. *A. tepida*, *C. excavatum* and *C. gunteri* was modified on 9 and 22 June but recovered on 4 August (Appendix A).

Figure 7

3.7. Size-frequency distributions of *Ammonia tepida*

Temporal changes in the size-frequency distributions of *Ammonia tepida* from both the 0-0.5 and the 0.5-1 cm layers are shown in Fig. 8. On 22 April, small individuals (175-275 μm in diameter) dominated the population in the 0-0.5 cm layer, whereas bigger specimens (300-475

μm) were also abundant in the 0.5-1 cm layer (K-S test results: $P < 0.001$). Over April and May, specimens grew and 425-500 μm specimens dominated both histograms from 25 May. However, these histograms significantly differed from each other due to a higher proportion of bigger specimens within surface sediments (K-S test results: $P < 0.001$). Major mortalities occurred between the end of May and 9 June leading to size-frequency distributions between the two sediment layers becoming homogeneous (K-S test results: $P = 0.23$). At the end of June, size-frequency distributions of the two sediment layers differed in the occurrence of large specimens ($> 450 \mu\text{m}$ in length) in 0.5-1 cm depth which led to a significant difference between the layers (K-S test results: $P < 0.05$). On 4 August, huge numbers of juveniles occurred only in the surface sediment layer, while larger specimens dominated the *A. tepida* population of the 0.5-1 cm depth (Fig. 8, K-S test results: $P < 0.001$).

Figure 8

4. Discussion

4.1. Microdistribution of living (stained) foraminifera

It is well known that patchiness may be an important issue, particularly in stressed, shallow systems like intertidal mudflats. The microdistribution of foraminifera may induce bias, especially on absolute abundances (see a review in Morvan, Debenay, Jorissen, Redois, Bénéteau, Delplancke et al., 2006). Most authors (e.g. Alve & Murray, 2001; Licari, Schumacher, Wenzhöfer, Zabel & Mackensen, 2003) made replicates when they used core sampling method. In contrast, a study on salt marsh foraminifera microhabitats by Goldstein, Watkins & Kuhn (1995) had only a single core per sampling site. In the present study, the potential bias due to small-scale patchiness of foraminifera was tested by using two different sampling methods. The t-tests for paired data indicate that similar results were obtained with both methods. This suggests that small-scale patchiness of foraminifera does not affect

significantly the results in the study site during the sampling period and that the collection of a single core per sampling date did not induce significant biases.

4.2. Short-term hypoxic conditions

From the end of May to mid-June, the geochemical characteristics at the water-sediment-interface and within the sedimentary column underwent marked changes. A sudden decrease in Chl *a* concentrations occurred during the second week of June. An increase in POC and PON values was found on 9 June and hypoxic conditions in the water column from 25 May to 9 June (Table 1). At the same time, high concentrations of dissolved ammonia, which is composed of un-ionised ($\text{NH}_3\text{-N}$) and ionised forms (NH_4^+), were recorded in the sediment porewater in the upper horizons of sediment cores. The anaerobic oxidation of organic nitrogen yielded the un-ionised form which is the most toxic to aquatic organisms (Kir, Kumlu & Eroldogan, 2004). A decrease in microphytobenthos concentrations occurred also when the NH_4^+ concentrations were the highest. Important amounts of biodeposits, which accumulated during autumn and winter under the oyster culture tables (Lerat et al., 1985), led to organic enrichment of the sediment (Sornin et al., 1983; Ottman & Sornin, 1985), followed by remineralisation. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the top 1 cm of sediments also confirmed that oyster biodeposits contribute to the organic enrichment of the sediment (Feuillet-Girard, Héral, Abrioux & Fontugne, 1994; Riera et al., 1996; Kang, Sauriau, Richard & Blanchard, 1999). In association with the increasing temperatures during spring and early summer diurnal emersions, the remineralisation of accumulated organic matter on intertidal mudflats is accelerated (Mazouni, Gaertner, Deslous-Paoli, Landrein & Geringer d'Oedenberg, 1996; Vouvé et al., 2000). Sediment-water exchanges were altered and short-term sediment anoxia likely occurred within surface sediments. Feuillet-Girard et al. (1988) indicated that sediment anoxia permits NH_4^+ fluxes from the sediment to the water column. Santschi et al. (1990)

reported the redox sequence commonly observed in time and space. A value of -160 mV is characteristically observed at 40 cm depth, associated with sulphate reduction. However, we observed this value at only 1 cm depth. Anaerobic processes occurred at very shallow depths, due to enhanced remineralisation which produced sulfide in the topmost layers on 1 June. Thus, both organic enrichment by oyster cultures and seasonal warming induced an alteration of the biochemical cycles in the sedimentary column.

4.3. Temperature, hypoxia and ammonium: limiting factors for living foraminifera

As seen previously, high temperatures and hypoxic waters characterised the critical period from the end of May to mid-June. This environmental disturbance strongly affected living (stained) foraminiferal assemblages through significant modifications in the density and the population structure between 25 May and 9 June, and may have contributed to the maximum of mortality for oysters that occurred from early to mid-June.

Large amounts of organic matter in the sediments and high temperatures are known to enhance foraminifera development. Lee & Müller (1974) demonstrated that the optimal range of temperature for reproduction of coastal species is between 20 and 30°C. The generation time of *Ammonia tepida* shifts from 88 days at 20°C, to 33 days at 30°C (Bradshaw, 1961). In our study however, the temperature range previously found most favourable for foraminifera reproduction coincided with the period of maximal decline in foraminifera abundances. Temperatures were not high enough to explain such a mortality, which could be explained by a synergetic effect of several deleterious parameters. The combination of a general increase and diurnal pulses in temperature may boost the remineralisation of accumulated organic matter (Vouvé et al., 2000). This remineralisation consumes oxygen and may in turn lead to oxygen depletion in the ambient water and the surface sediment porewater. Thus, temperature may have a paradoxical effect on living foraminifera such that temperature enhances the

reproduction until a critical value above which it becomes an indirectly limiting factor through its influence on biogeochemical processes.

Oxygen is a prime factor controlling and structuring benthic ecosystems, including their foraminiferal assemblages (den Dulk et al., 2000). Depending on the level of oxygenation, sensitive species of foraminifera may or may not be present. For instance, *Elphidium magellanicum* and *Stainforthia fusiformis* are oxytolerant species (Alve, 1995a; Gustafsson & Nordberg, 2000). In this study, hypoxic conditions (20 % air-saturated water, Eh=-160 mV) occurred from 26 May and 10 June. Simultaneously, the structure of the foraminiferal assemblages was modified.

From the RFDs established for the three layers (0-0.5, 0.5-1 and 5-8 cm), it appeared that foraminiferal assemblages in the topmost sediments were more affected than those in the deepest which were equally dominated by two species for the entire survey period. Changes in RFDs are sensitive to events that affects dynamics of foraminiferal populations such recruitment and mortality. Large recruitment of a dominant species increases both its abundance and rank and lead to a shift in RFDs from intermediate or mature stages (curves 2 and 3) to pioneer stage (curve 1). In the uppermost slice, the living foraminiferal assemblage was at a mature stage on 22 April and five species dominated: *Ammonia tepida*, *Brizalina striatula*, *Haynesina germanica*, *Criboelphidium excavatum* and *Quinqueloculina seminula*. This assemblage was subsequently altered by 9 June and species dominances were similar to those of deeper layers. At the same time, only *A. tepida* dominated the assemblages. The other species declined but did not disappear totally. From late June, a recovery in environmental conditions allowed regeneration and reorganisation of the living foraminiferal assemblages dominated by large recruitments of juvenile *A. tepida*. Contrary to the topmost layers, benthic foraminiferal assemblages in the 5-8 cm slice were not modified during the hypoxic crisis recorded in surface sediment. RFDs indicated that the assemblages were constant in shape,

with *A. tepida* and *C. excavatum* as the dominant species, on all sampling dates. Environmental conditions in the 5-8 cm slice remained fairly similar during the study, and the same two species appeared to be tolerant of the anoxia that occurs regularly at this level.

4.4. *Haynesina germanica* and *Brizalina striatula* (sensitive species), *Ammonia tepida* (tolerant species) and *Criboelphidium gunteri* (pioneer species)

Many foraminiferal species have been reported to be tolerant to oxygen depletion and organic matter enrichment. For instance, Bernhard (1993) indicated that meiofauna taxa (ostracoda, nematods and copepods) totally disappear during anoxia whereas living foraminifera were tolerant to short periods of anoxia and sulfide fluxes. The living benthic foraminiferal assemblages described in our study illustrate their resistant capacity, e.g. *Ammonia tepida* dominated the stained assemblage during the whole sampling period with an average occurrence of 80 %. Samir (2000), in his study on the foraminiferal assemblages of the Nile delta, also reported *A. tepida* as the most tolerant species in environments submitted to organic pulses. Armynot du Châtelet, Debenay & Soulard (2004) reported the same characteristic for *A. tepida* in their study on foraminiferal assemblages in moderately polluted harbours. Moreover, although its abundances declined, *A. tepida* was able to regenerate rapidly as a recruitment of juveniles occurred in August, characterised by individuals with three chambers or fewer.

The abundances of *Haynesina germanica* and *Brizalina striatula*, however decreased significantly and rapidly during the hypoxia event. They appeared to be sensitive to organic degradation and anoxia, in contrast to Armynot du Châtelet et al. (2004) and Debenay, Millet & Angelidis (2005) description of *H. germanica* as tolerant to organic matter enrichment. Thus, both hypoxia and high ammonia concentrations may be the main variables explaining the decline of *H. germanica*. Observations of living foraminiferal assemblages on 4 August,

showed that the abundance of *Criboelphidium gunteri* had increased significantly whereas the abundances of the other species were still low and *C. gunteri* had become the dominant species together with *A. tepida*. Debenay et al. (2006) reported *C. gunteri* as a pioneer species. Moreover, Boudreau, Patterson, Dalby & McKillop (2001) reported this species to occur in fresh waters showing its great adaptability to various environmental conditions. In their study, they observed a rapid development of *C. gunteri*, and concluded that it is a pioneer species. *C. gunteri* appears better specialised for colonisation and dispersal than the other species in this study.

5. Conclusion

The remineralisation of the organic matter that had accumulated under the oyster racks was controlled by the seasonal warming. This occurred in conjunction with an hypoxic crisis in the water column at the beginning of the warmest season. We have found that living (stained) foraminiferal assemblages in the topmost layer were significantly altered during this warm-season hypoxic event, and that living (stained) foraminiferal responses were species specific. *Haynesina germanica* and *Brizalina striatula* are sensitive to hypoxia and ammonia concentration and changes in their abundance may be considered as good proxies for such events. However, sensitive species did not totally disappear. *Ammonia tepida* appears as a tolerant species capable of regenerating its abundances rapidly and *Criboelphidium gunteri* appears as a pioneer species able to rapidly colonize the topmost sediment layers after the warm-season hypoxic event. These results from living (stained) foraminiferal dynamics and assemblage structures finally support the idea that toxic changes in sediment biochemistry are involved in Pacific oyster summer mortalities.

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Figure legends

Figure 1. Map of the Marennes-Oléron Bay with the location of the Ronce-Perquis sampling site

Figure 2. Time series of turbidity (grey line) and oxygen content as % air-saturation (black line) in the water column at 15 cm above the sediment surface at the oyster culture site of Ronce-Perquis from 22 April to 23 June.

Figure 3. Temperature time series at the sediment-water interface (grey line) and 15 cm sediment depth (black line) at the oyster culture site of Ronce-Perquis from 22 April to 4 August. Day-to-day changes in the tidal coefficient (see text for definition, dashed line) are shown together with mortality rate (% day⁻¹; scale X 10) of oysters from “on-bottom” (filled circle) and “off-bottom” (open square) culture conditions.

Figure 4. Temporal changes in depth profiles of porewater ammonium and sulfide contents (mg l⁻¹) within sediment cores sampled at Ronce-Perquis from 22 April to 4 August.

Figure 5. Changes in species richness and abundances of living (stained) foraminifera with depth of sediment cores sampled at Ronce-Perquis from 22 April to 4 August.

Figure 6. Abundances of *Ammonia tepida* (a), *Brizalina striatula* (b), *Criboelphidium excavatum* (c), *Criboelphidium gunteri* (d), *Haynesina germanica* (e) and *Quinqueloculina seminula* (f) at 0-0.5 (white) and 0.5-1 cm depth (grey) of sediment cores sampled at Ronce-Perquis from 22 April to 4 August.

Figure 7. Benthic foraminifera rank-frequency diagrams at 0-0.5 (a), 0.5-1 (b) and 5-8 cm depth (c) of sediment cores sampled at Ronce-Perquis from 22 April to 4 August and theoretical RFD curve shapes (d, 1: linear-concave = pioneer assemblage, 2: convex = intermediate assemblage and 3: straight-line = mature assemblage, dotted arrow = example of ecological succession: recovery in the assemblage).

Figure 8. Changes in *Ammonia tepida* size class frequencies at 0-0.5 (a) and 0.5-1 cm depth (b) of sediment cores sampled at Ronce-Perquis from 22 April to 4 August and P values are statistics for K-S test.

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Table 1. Changes in water salinity and in sediment parameters from 22 April to 4 August 2004 (nd: no data).

Sample date		4/22/2004	4/26/2004	5/6/2004	5/25/2004	6/9/2004	6/14/2004	6/22/2004	6/30/2004	8/4/2004
Salinity		32	31	33	34	35	34	34	nd	nd
T (°C)	1 cm	nd	nd	nd	20	27	18	27	nd	26
	4 cm	nd	nd	nd	20	25	19	25	nd	24
pH	1 cm	nd	nd	nd	7.1	7.3	7.6	7.4	nd	6.9
	4 cm	nd	nd	nd	7.4	8.0	7.9	8.0	nd	7.4
Eh (mV)	1 cm	nd	nd	nd	-146	-153	-155	-160	nd	-112
	4 cm	nd	nd	nd	-183	-176	-178	-175	nd	-123
Chl <i>a</i> (mg m ⁻²)	0-1 cm	285 ± 8	262 ± 87	335 ± 22	409 ± 264	864 ± 12	313 ± 58	310 ± 57	634 ± 325	757 ± 99
	1-2 cm	nd	nd	224 ± 38	272 ± 57	314 ± 68	142 ± 43	173 ± 45	304 ± 70	210 ± 58
Phaeopigments (mg m ⁻²)	0-1 cm	442 ± 12	422 ± 170	633 ± 90	611 ± 225	1586 ± 702	383 ± 37	411 ± 69	717 ± 92	998 ± 300
	1-2 cm	nd	nd	494 ± 69	550 ± 78	648 ± 111	218 ± 65	269 ± 90	648 ± 132	435 ± 125
POC (μg mg ⁻¹ dry sediment)	0-1 cm	5.50	5.83	5.05	5.35	8.78	4.61	5.63	6.73	9.67
	1-2 cm	nd	nd	4.43	5.80	6.66	3.68	5.28	7.49	5.70
PON (μg mg ⁻¹ dry sediment)	0-1 cm	0.76	0.78	0.71	0.81	1.26	0.66	0.83	1.00	1.44
	1-2 cm	nd	nd	0.65	0.81	0.92	0.55	0.77	0.98	0.81
C/N ratio	0-1 cm	7.2	7.5	7.1	6.6	7.0	7.0	6.8	6.7	6.7
	1-2 cm	nd	nd	6.8	7.1	7.2	6.7	6.9	7.6	7.0
δ ¹³ C (‰)		-21.8	-21.5	-21.5	-21.1	-20.7	-20.6	-21.3	-20.5	-20.8
δ ¹⁵ N (‰)		6.2	6.2	6.2	5.9	6.2	6.1	5.9	6.4	6.3

Table 2. Characteristics of the six main living (stained) species from the pseudoreplication samples (PS) and from the core samples (CS) from 0-0.5 cm sediments. Total number of living test (abundance), species richness and abundances of each species per sample from 22 April to 4 August 2004 in 50 cm³ of sediment and P values are statistics for Student t-test for paired data.

Sample date Method	04/22/2004		05/25/2004		06/09/2004		06/22/2004		08/04/2004		Student t-test P
	PS	CS	PS	CS	PS	CS	PS	CS	PS	CS	
Abundance (stained)	16844	10365	5855	6629	7709	4686	3720	10146	5257	10295	0.83
Species richness (stained)	12	14	8	8	7	8	11	9	8	7	0.99
<i>Ammonia tepida</i>	12807	5688	4960	4184	7188	3218	2530	6956	3235	6806	0.74
<i>Brizalina striatula</i>	550	1338	448	363	52	428	174	797	168	294	0.08
<i>Criboelphidium excavatum</i>	2459	658	224	1640	156	693	74	665	303	252	0.81
<i>Criboelphidium gunteri</i>	330	82	37	0	52	142	223	310	1112	2438	0.43
<i>Haynesina germanica</i>	183	973	75	78	52	82	0	133	135	126	0.28
<i>Quinqueloculina seminula</i>	220	647	37	130	156	0	521	930	135	336	0.15

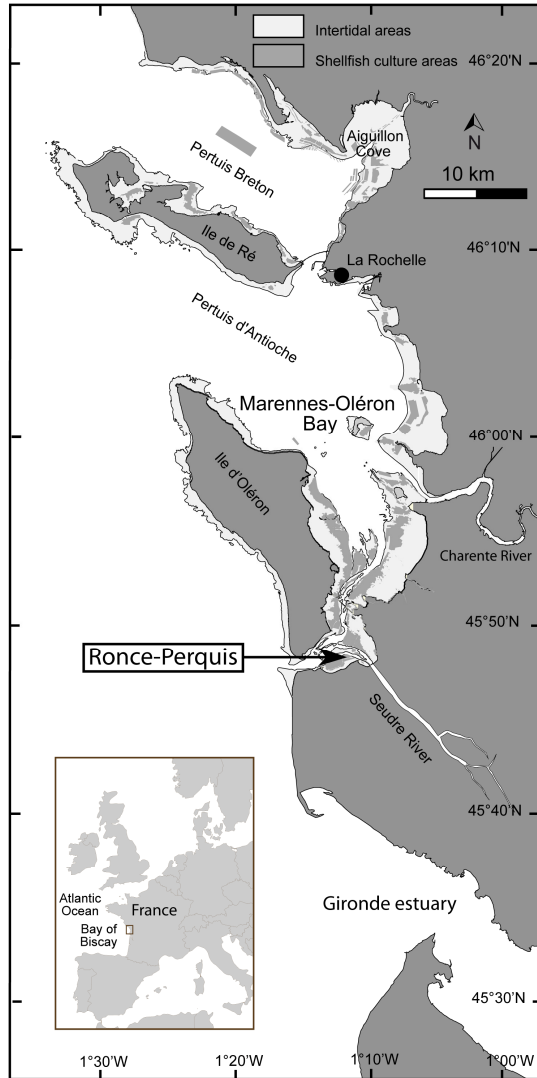


Fig 1

Figure 2

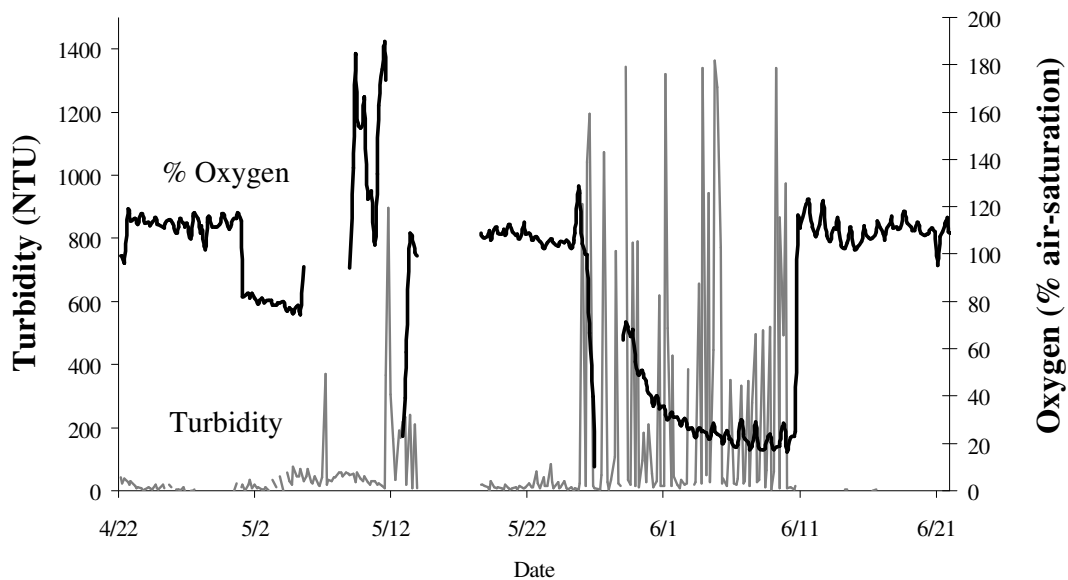


Fig 3

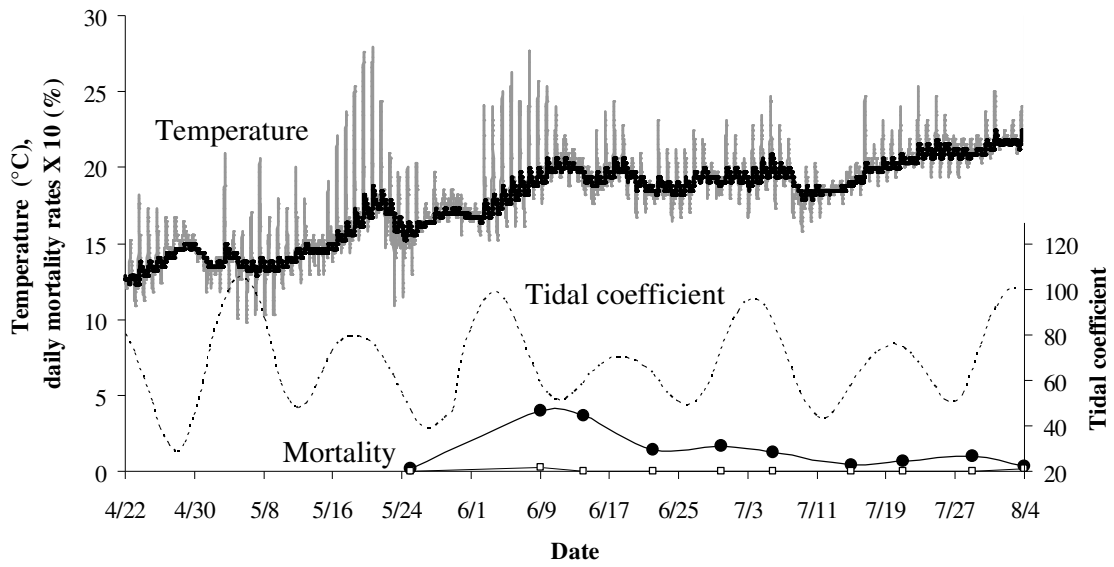


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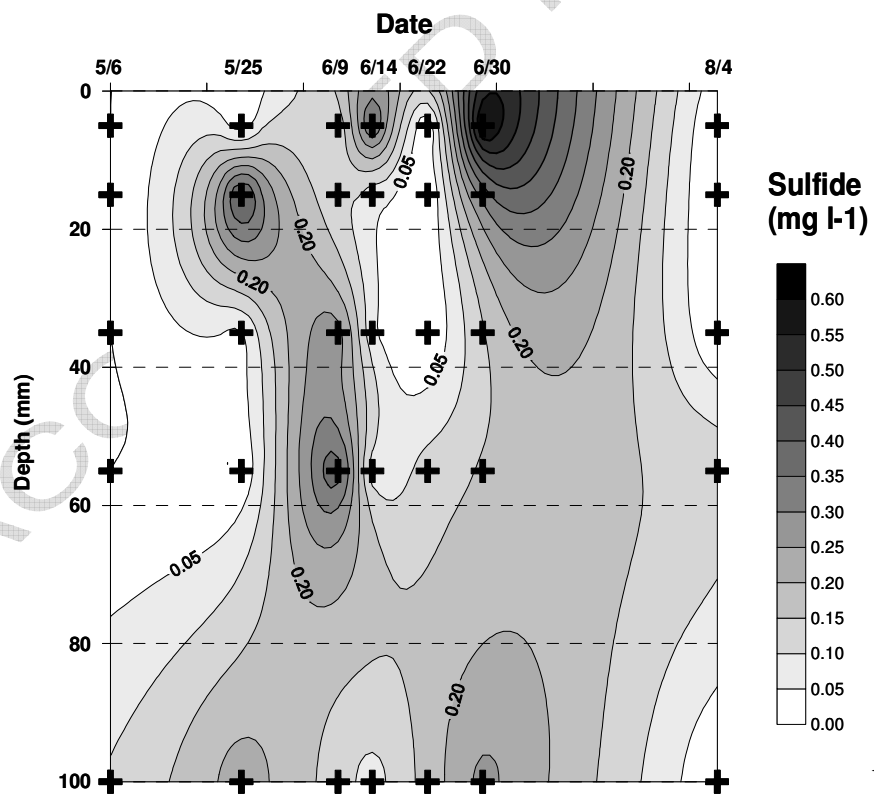
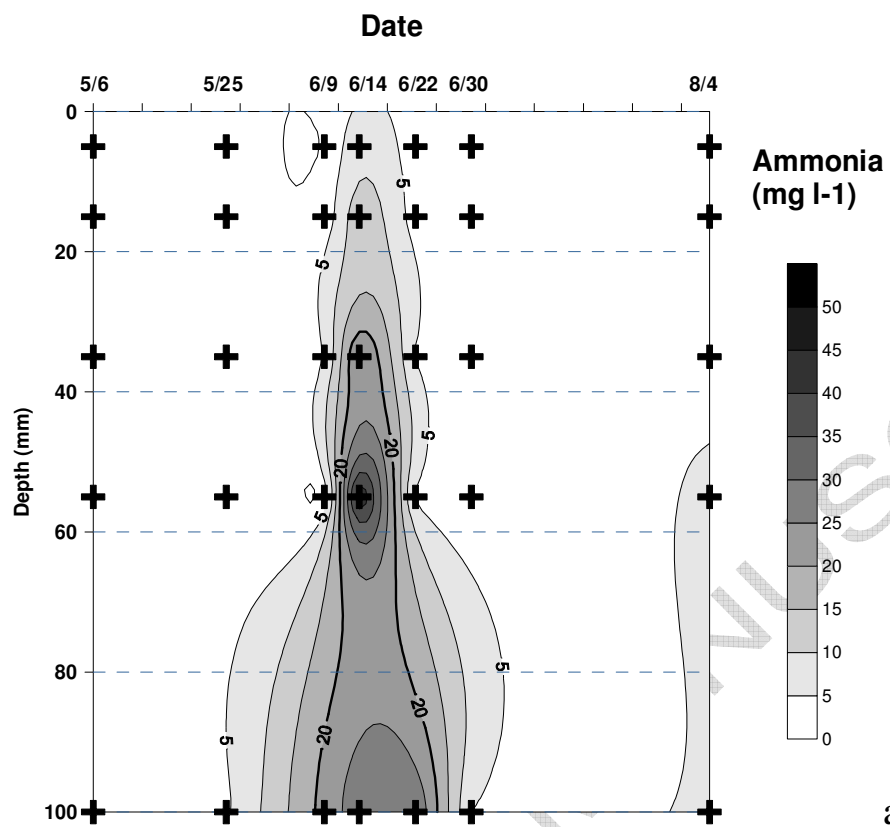


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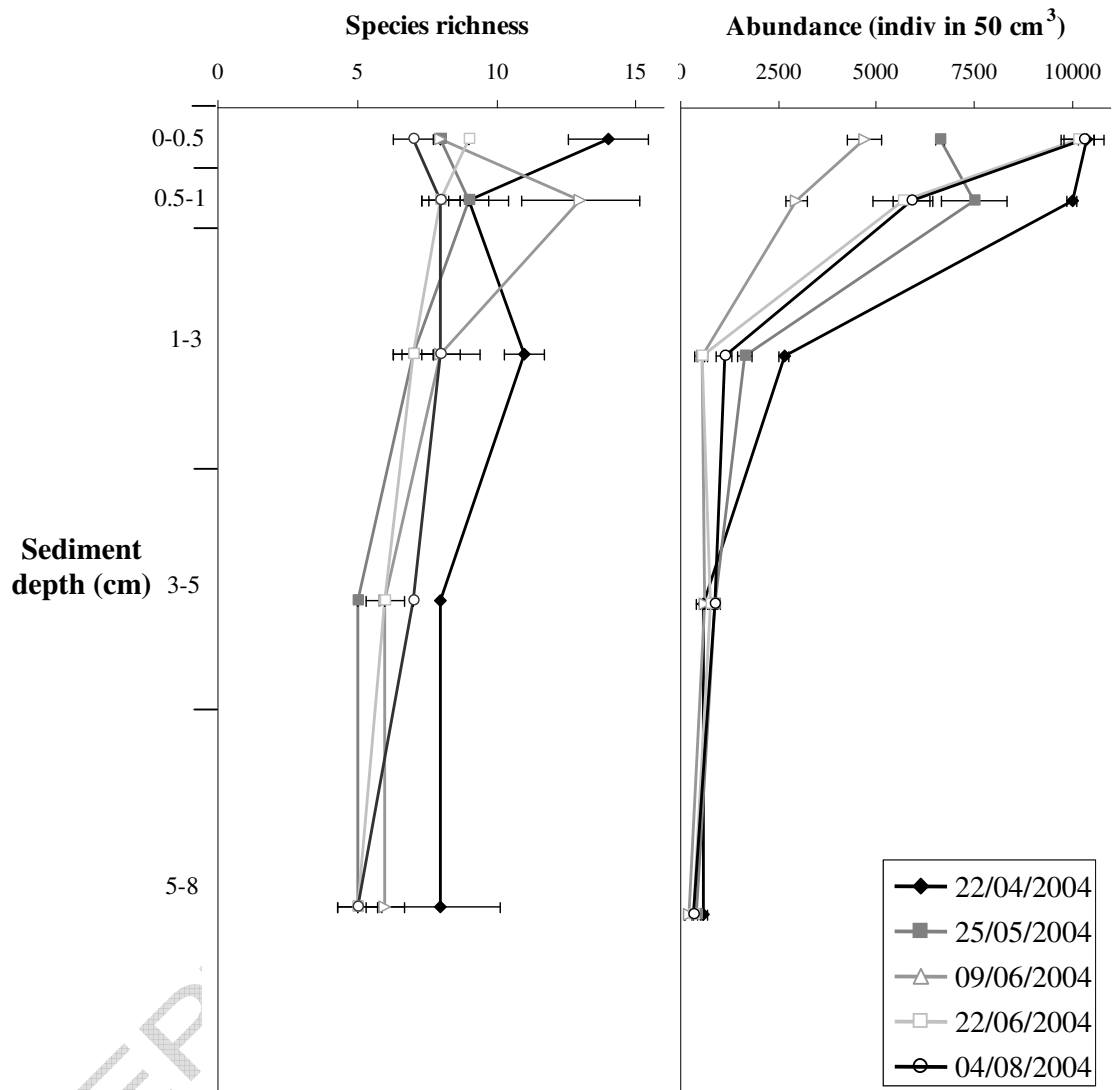


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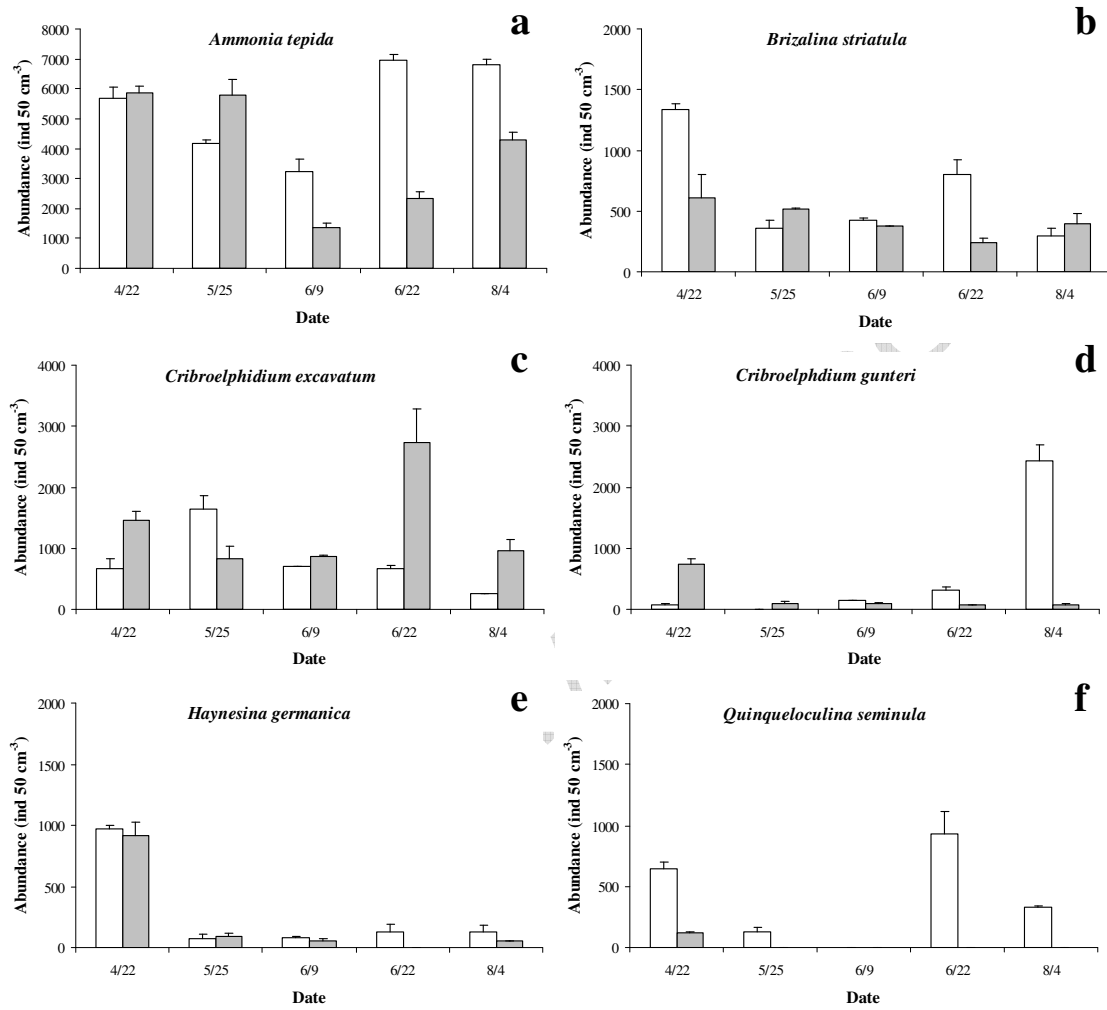


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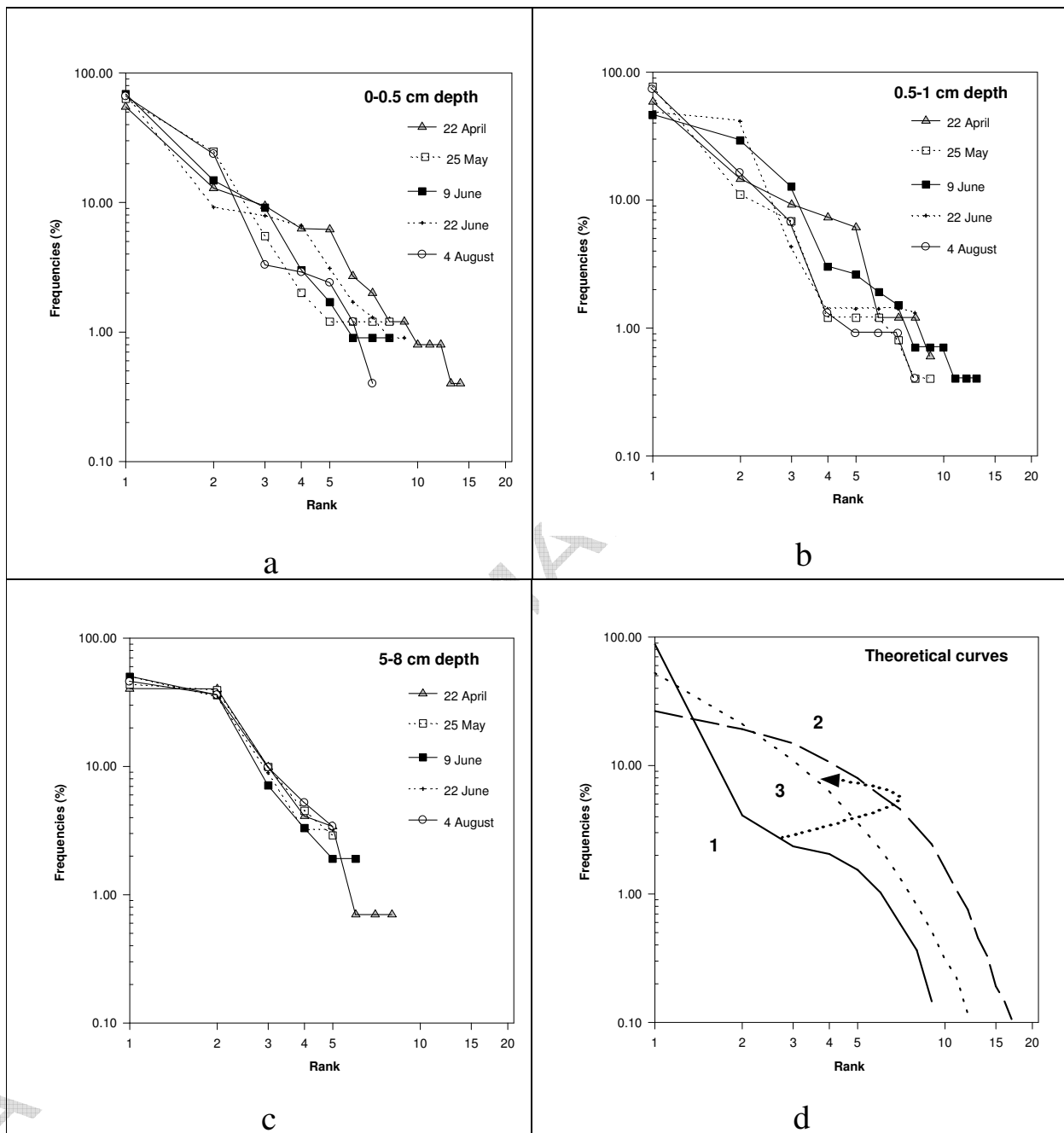
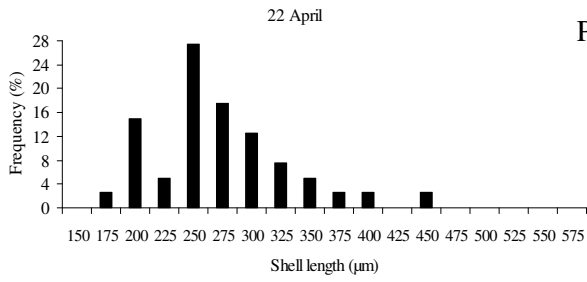
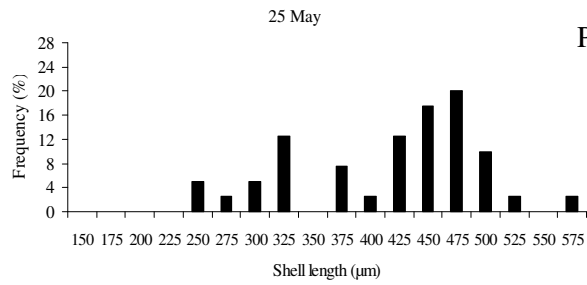
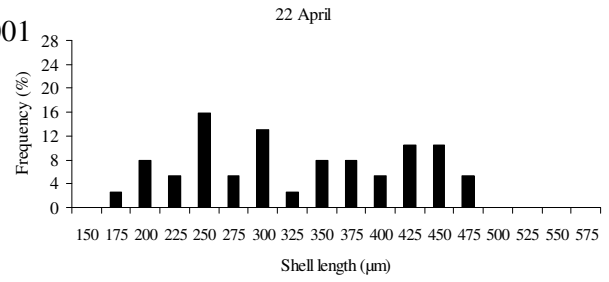
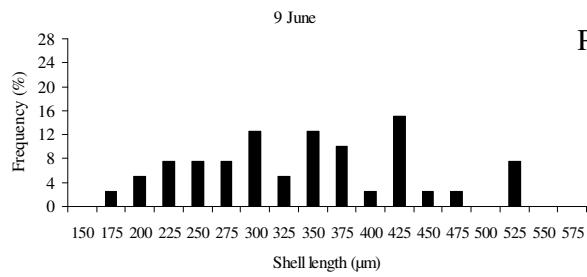
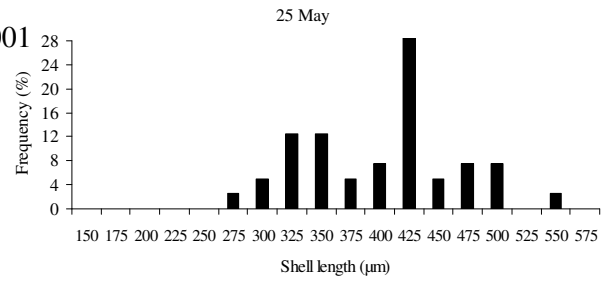
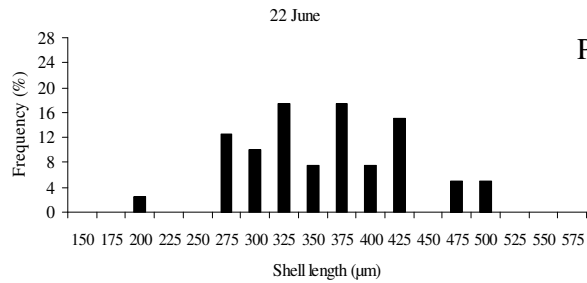
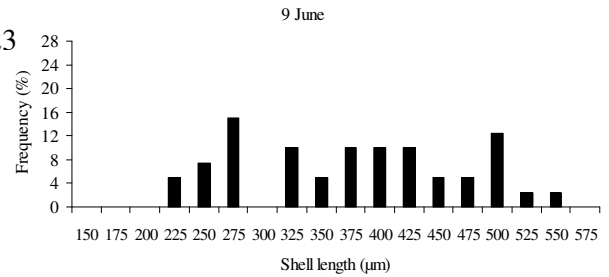
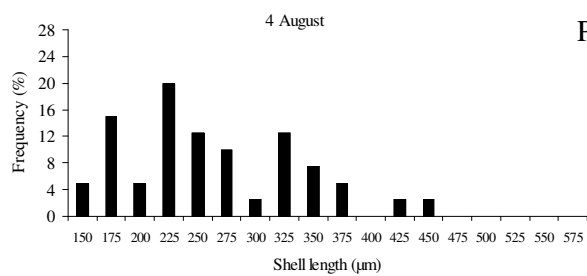
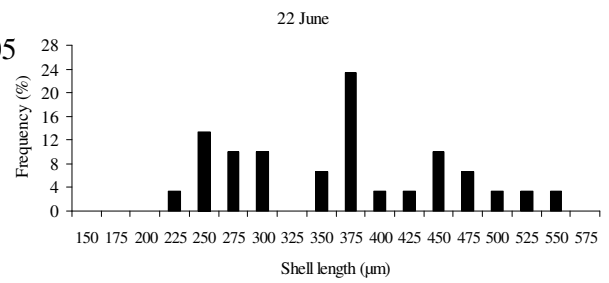


Fig 8

0-0.5 cm depth (a)

0.5-1 cm depth (b)

 $P < 0.001$  $P < 0.001$  $P = 0.23$  $P < 0.05$  $P < 0.001$ 