

Trophic interactions between two introduced suspension-feeders, *Crepidula fornicata* and *Crassostrea gigas*, are influenced by seasonal effects and qualitative selection capacity

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Abstract

The effects of season and qualitative selection capacity on trophic relationships between two sympatric invasive suspension-feeders, *Crepidula fornicata* and *Crassostrea gigas*, were investigated in Bourgneuf Bay (France) from January 2003 to June 2004. Carbon and nitrogen stable isotopic deviations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, of common Atlantic slippersnails and Pacific oysters were analysed relative to isotopic composition and availability of end-members.

Slippersnail deviations were less variable over the sampling period compared with those of oysters. Significant differences between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *C. fornicata* and *C. gigas* were found from winter to early summer, and linked to major isotopic changes in oysters. We identified three distinct seasonal periods: January to March when oysters were ^{15}N -enriched compared to slippersnails and to themselves at other times of the year, April to June–July when oysters showed a ^{15}N -depletion and a more marked ^{13}C -depletion compared to slippersnails and to themselves at other times of the year, and July–August to December when both species presented similar carbon and nitrogen deviations. Species-specific differences in qualitative selection capability may explain these seasonal differences in isotopic deviations. Whereas the isotopic composition of the indiscriminate suspension-feeding slippersnails reflects the composition of the seston throughout the year, the oyster is capable of qualitative selection. The oyster isotopic compositions are consistent with a facultative activation of selection mechanisms under conditions of qualitative and quantitative food limitation, notably the preferential ingestion and assimilation of the dominant organic source in the suspended pool.

We conclude that *C. fornicata* and *C. gigas* are trophic competitors only in winter and spring at this site, where detrital end-members are major POM components. These results underscore (1) the importance of long-term (annual) studies in the evaluation of potential trophic competition, and (2) the necessity to include the qualitative selection capacities of suspension-feeders in future interpretations of trophic relationships in marine coastal ecosystems.

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1. Introduction

Human activity has increasingly promoted dispersal and colonization of exogenous marine organisms. When

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these species become invasive, they change the structure and function of surrounding communities and ecosystems (Carlton, 1989; Grosholz, 2002; Occhipinti-Ambrogi and Savini, 2003). Invaders may also become pest species for aquaculture, as trophic competitors, predators or disease vectors (Ruesink et al., 2005).

The common Atlantic slipper snail *Crepidula fornicata* and the now-ubiquitous Pacific oyster *Crassostrea gigas* are two sympatric invaders of human-impacted European littoral habitats, where their proliferation is encouraged directly or indirectly by aquaculture activities (Blanchard, 1997; Ruesink et al., 2005). The two species have not only attained considerable biomasses from Scandinavian to Mediterranean countries (de Montaudouin et al., 2001; Thieltges et al., 2003; Ruesink et al., 2005; Cognie et al., 2006), but have also generated ecological consequences such as alterations of benthic habitats and communities, or food chain changes (e.g. Ehrhold et al., 1998; Ruesink et al., 2005; Thieltges, 2005; Wonham et al., 2005). Competitive dominance of *C. fornicata* has long been suspected (Murie, 1911; Orton, 1912a; Korringa, 1951; Cole and Hancock, 1956), generating increasing concern regarding the eventual negative effect of slipper snails on native or introduced oyster productions (Trochon, 1954; Marteil, 1963; Deslous-Paoli, 1985; Deslous-Paoli and Héral, 1986; Crepel, 1994; Blanchard, 1997; Sauriau et al., 1998; de Montaudouin et al., 1999; Riera et al., 2002).

The impact of suspension-feeders on the seston assemblage will depend not only upon their quantitative filtration ability, but also on their capacity to ingest or reject particles selectively (see review by Ward and Shumway, 2004). Selection may be based on non-nutritive criteria such as size, density and shape (hence determining the types of particles physically able to be processed by the feeding structures — Bougrier et al., 1997; Defossez and Hawkins, 1997). Selection may also be based on the biochemical characteristics of particles; being potentially related to nutritive quality, such selection is termed qualitative (Targett and Ward, 1991; MacDonald and Ward, 1994; Beninger et al., 2004). Particle selection capability will therefore be an important determinant of resource partitioning among different suspension-feeders. Although *C. fornicata* and *C. gigas* access the same pools of suspended particulate organic matter (Orton, 1912a,b; Walne, 1956; Deslous-Paoli, 1985), fundamental differences in their feeding characteristics may influence the degree of trophic competition. Indeed, *C. fornicata* presents lower clearance rates, but they retain particles over the same size range as *C. gigas*, with a marked superiority in particles $< 5 \mu\text{m}$ (Jørgensen et al., 1984; Méléder et al., 2001; Barillé et al., 2006; Sauriau et al., 2006). An essential difference exists between these two suspension-feeders, however, with respect to the qualitative selection of seston particles: *C. fornicata* is an indiscriminate suspension-

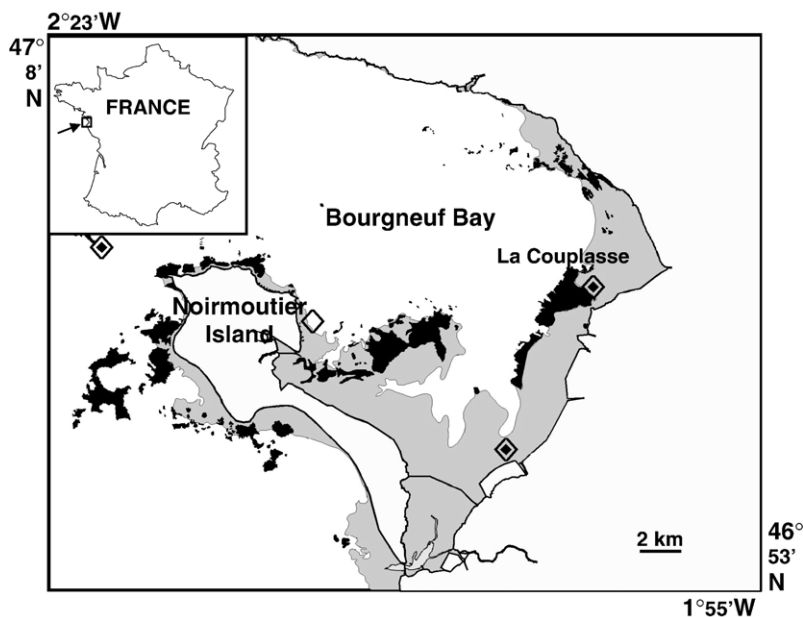


Fig. 1. Map of Bourgneuf Bay showing location of La Couplassse oyster farming site, source (◊) and REPHY (◇) sampling stations. Grey shading: intertidal area; black shading: rocky substrate.

feeder (Beninger et al., in press), whereas *C. gigas* is capable of qualitative particle selection (Ward et al., 1998; Cognie et al., 2003). Moreover, the scant literature to date on diets of these two species (Riera et al., 2002; Decottignies et al., in press) has underscored differences in exploitation of natural food sources.

In coastal and estuarine sedentary suspension-feeding organisms, temporal and spatial fluctuations in the quantity and the composition of seston engender ecophysiological optimization responses (e.g. Bayne et al., 1993; Barillé et al., 1997; Cranford and Hill, 1999; Navarro et al., 2003). It may thus be proposed that these responses are important determinants of trophic partitioning, and may be related to the success and proliferation of *C. fornicata* and *C. gigas*. In particular, the differential qualitative selection capacities of these two species (Beninger et al., in press) may be expected to

produce distinct seasonal differences in resource use, related to fluctuations in source abundance.

Using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopic compositions of sources and suspension-feeders, the present study reports on long-term, seasonal variations in the trophic sources of co-occurring *C. fornicata* and *C. gigas* in the oyster — farming intertidal mudflat of Bourgneuf Bay (France), in the light of the fundamental difference in suspension-feeding mechanisms (indiscriminate vs. selective).

2. Materials and methods

2.1. Sampling and preparation for isotopic analyses

Five Pacific oysters (mean shell length = 10.0 ± 1.7 cm) and five slippersnails (mean linear shell length = 3.3 ± 0.4 cm) were sampled monthly in Bourgneuf Bay (French

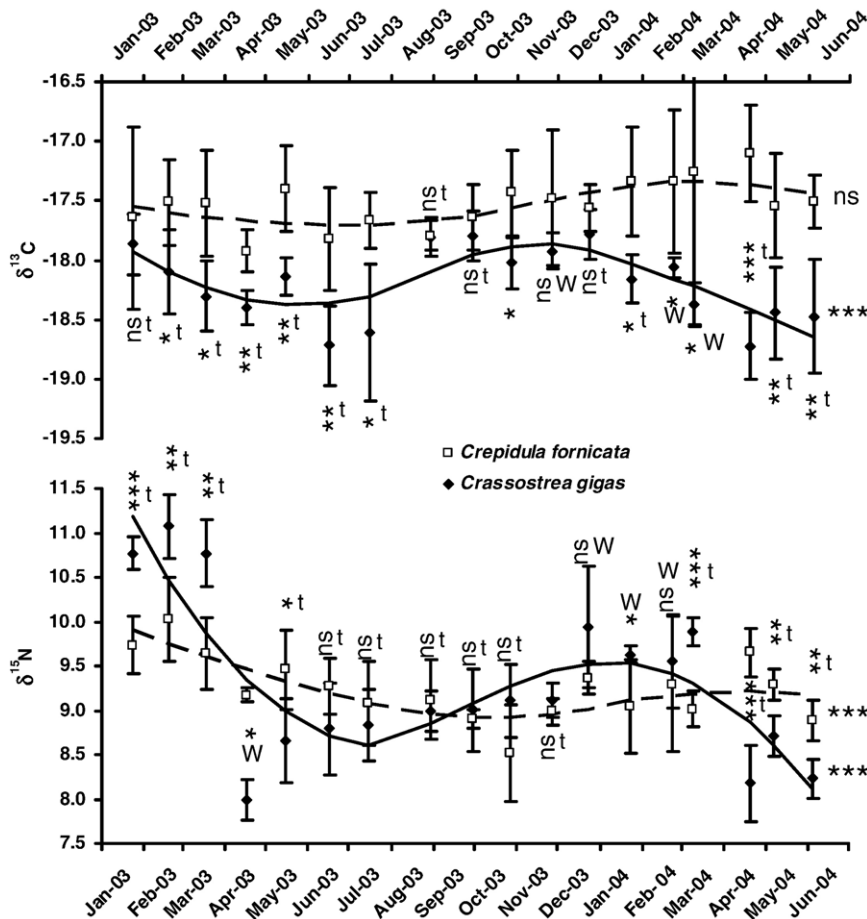


Fig. 2. Seasonal evolution of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm SD) of *Crepidula fornicata* and *Crassostrea gigas*. Horizontal asterisks indicate significant intraspecific differences on the studied period (Kruskal–Wallis). Vertical asterisks show significant interspecific differences (*t*-test (t) and Wilcoxon test (W) for parametric and non-parametric data sets, respectively). ns $p > 0.05$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Loess curves are represented by the dashed line for *C. fornicata*, and the continuous line for *C. gigas*.

Atlantic Coast, 46–47°N, 1–2°W) at the oyster farming site of La Couplasse (Fig. 1) from January 2003 to June 2004. Specimens were cleaned of epibionts at the lab-

oratory, kept alive for 12–24 h in 0.2 µm filtered seawater from the sampling site to purge gut contents, and killed by freezing. Soft tissues were separated from the shells.

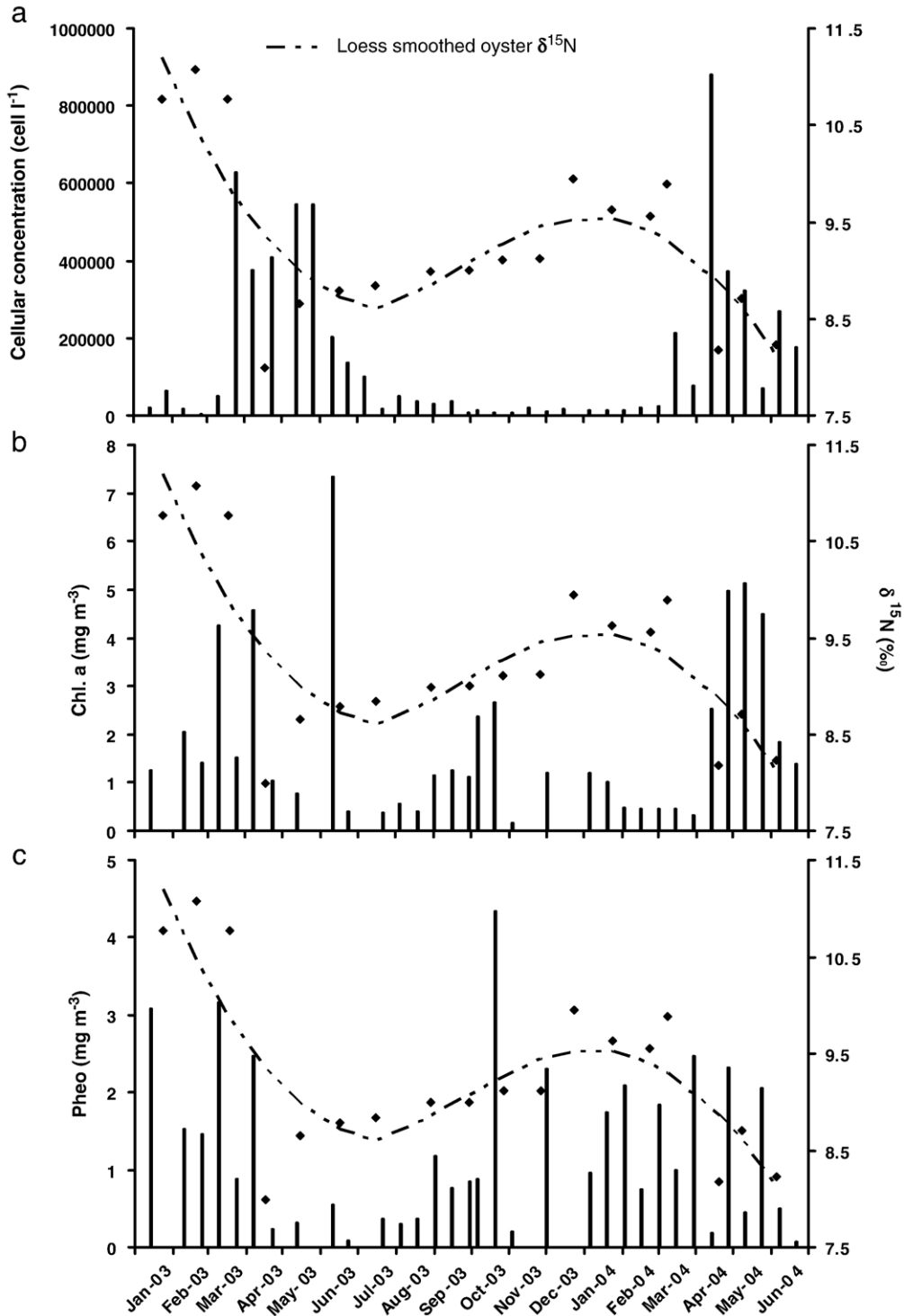


Fig. 3. Mean $\delta^{15}\text{N}$ variations of Pacific oysters in relation to phytoplankton data [cell (a), chlorophyll (b) and pheocipigment (c) concentrations — Ifremer REPHY Quadrigé database] over the study period.

The sources composing the end-members (benthic diatoms, marine particulate organic matter (POM), macroalgae and C_4 angiosperms, and C_3 angiosperms — Decottignies et al., in press) were collected seasonally within the bay (Fig. 1) in March, July and November 2003, and in February and June 2004. Twenty liters of sub-surface oceanic water samples were taken during sampling cruises off Noirmoutier Island and vacuum-filtered on triplicate GF/F pre-combusted (500 °C, 4 h) filters. The upper 5 mm layer of a 1 m², densely microphytobenthos-covered, mudflat area was collected and processed for benthic diatom extraction, as per Riera and Richard (1996) in order to also obtain triplicate filters. Macroalgal thalli pieces (*Enteromorpha* sp., *Fucus serratus* and *Fucus vesiculosus*) and marine angiosperm leaves (*Halimione portulacoides*, *Salicornia* sp. and *Spartina* sp.) were collected and cleaned of epibionts if necessary.

All samples were acidified 1 to 2 min with 1 M HCl to remove carbonates, rinsed with Milli-Q® ultrapure water, and stored at -80 °C prior to freeze-drying. Animal soft tissues and macrophytes were then reduced to a powder with a mortar and pestle prior to analysis.

2.2. Stable isotope analyses

Duplicate powdered samples or pieces of filters were sealed in ultraclean tin capsules and processed

for nitrogen and carbon stable isotope compositions, using a Carlo-Erba® NA 2100 elemental analyzer coupled, via a Thermo Finnigan® CONFLO II interface, with a Thermo Finnigan® Delta S mass spectrometer. Standard $\delta^{13}C$ and $\delta^{15}N$ (‰ deviations from Vienna Pee Dee Belemnite and atmospheric N₂, respectively) were calculated according to the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 10^3$, where X is either ^{13}C or ^{15}N and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. The $\delta^{13}C$ and $\delta^{15}N$ deviations of 200 analyses of a regularly calibrated working reference (acid glutamic), run every 11 samples, was 0.20‰ and 0.43‰, respectively. Analyses of the same sample duplicate capsules were validated if difference between calculated isotopic deviations was below 0.4 and 0.5‰ for carbon and nitrogen, respectively; otherwise, the samples were analyzed a second time.

Trophic fractionation values of 3.4‰ and 1‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, were used to correct for ^{15}N and ^{13}C enrichment from food to consumer (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002). Means of each end-member $\delta^{13}C$ and $\delta^{15}N$ over the entire sampling period were considered for diet contribution estimations. Contributions of each end-member to the two suspension-feeder diets were determined using IsoSource version 1.2

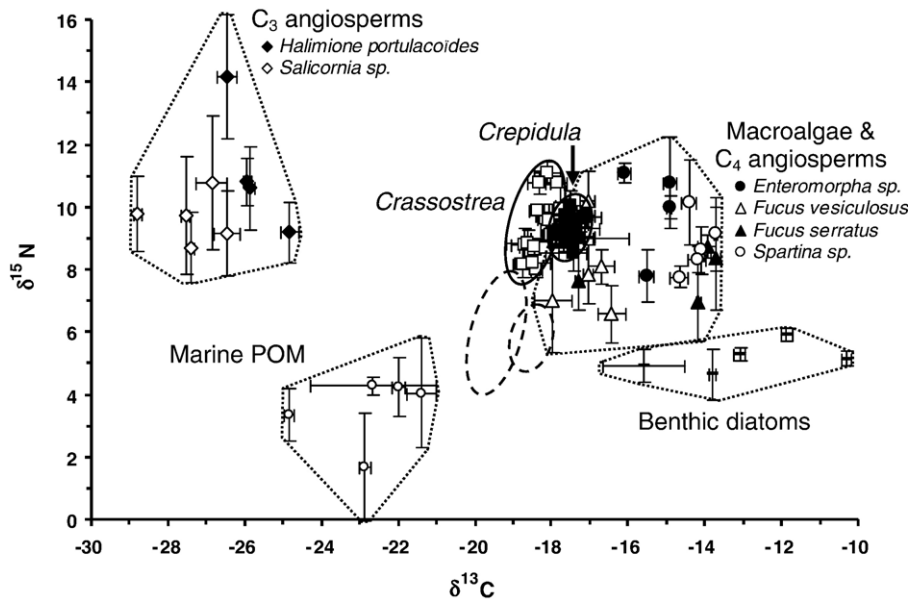


Fig. 4. Dual $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions (mean ‰ \pm SD) of sources (sampled every 3 months), and of *Crepidula fornicata* and *Crassostrea gigas* (sampled monthly) from January 2003 to June 2004. Continuous lines surround the dual isotopic deviations of the two suspension-feeders; whereas dashed lines surround the compositions of their calculated diets (obtained by subtracting trophic enrichments of 1 and 3.4‰ respectively (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002) from the $\delta^{13}C$ and $\delta^{15}N$ values of both species). Dotted polygons surround sources which composed the 4 end-members. POM: particulate organic matter.

software (Phillips and Gregg, 2003) with a 2-isotope multiple-source (i.e. end-member) mixing model, 1% increments and 0.2‰ tolerance. This software provides feasible biomass contributions which are consistent with isotopic mass balance.

2.3. REPHY data collection

The REPHY (REseau PHYtoplancton- <http://www.ifremer.fr/envlit/surveillance/rephy.htm>) is a long-term phytoplankton survey of French coastal waters conducted by the Institut Français de Recherche pour l'Exploitation de la MER (IFREMER), since 1984. In Bourgneuf Bay, the REPHY sampling station, called "Bois de la Chaise" (Code 28061004), is situated North-east of Noirmoutier Island (Fig. 1). Bimonthly concentrations of phytoplankton (number of cells per liter), chlorophyll *a* and phaeopigment (mg m^{-3}) were extracted from the REPHY Quadriège database between January 2003 and June 2004.

2.4. Statistical analysis

All statistical tests were run using R[®] freeware (R Development Core Team, 2005). As carbon and nitrogen isotopic deviations of each species were not normally distributed (Shapiro–Wilk tests) and/or characterized by heterogeneous variances (Bartlett tests), Kruskal–Wallis one-way non-parametric ANOVAs (hereafter called KW) were performed to test for eventual seasonal differences in compositions over the course of the sampling period. A local regression model, named "loess" (smoothing parameter=0.75) (Cleveland et al., 1992), was used to graphically depict $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ time fluctuations of *C. gigas* and *C. fornicata*. We also calculated the coefficient of variation (CV) of each data series (Sokal and Rohlf, 1995). Pacific oyster and common Atlantic slipper snail isotopic deviations were compared at each month, using either a Welch two sample *t*-test or Wilcoxon rank sum test, as appropriate according to data normality and homoscedasticity

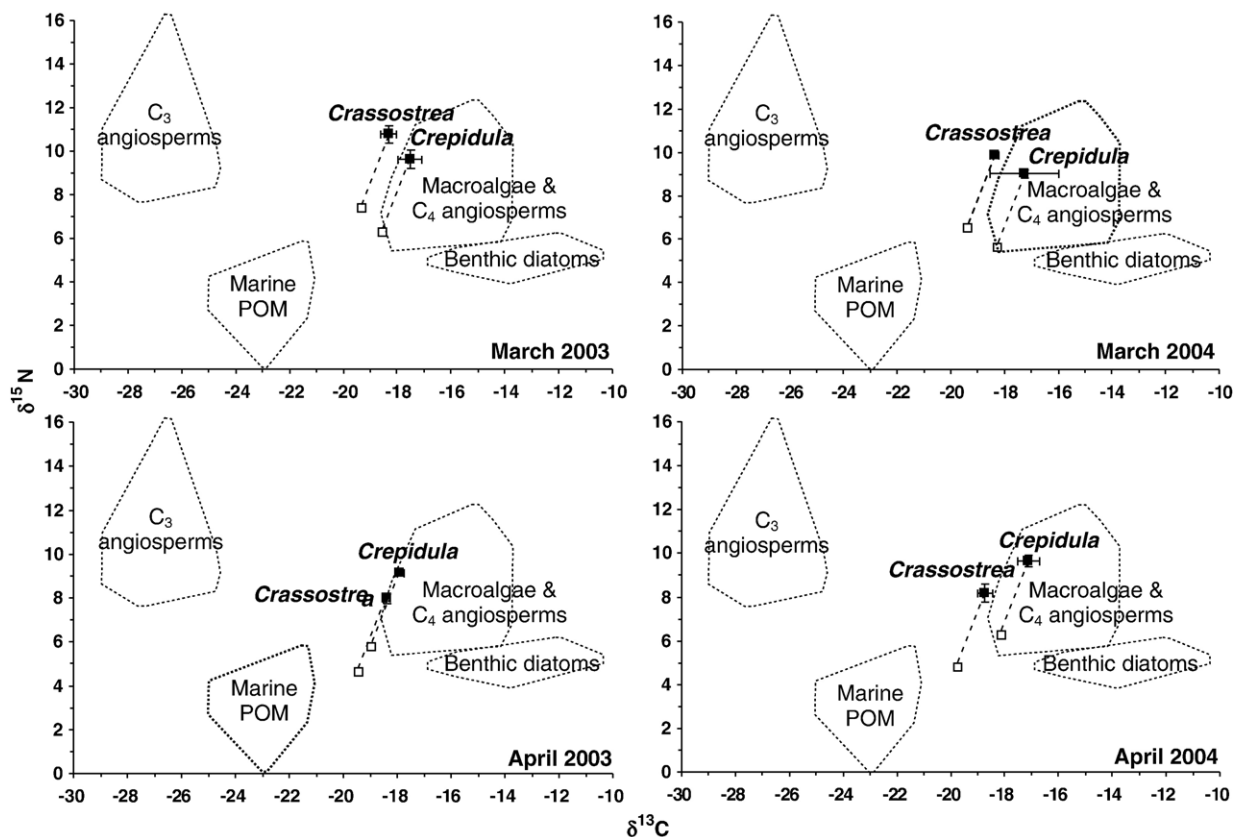


Fig. 5. Dual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic compositions (mean $\text{‰} \pm \text{SD}$) of *Crepidula fornicata* and *Crassostrea gigas* in March and April 2003 and 2004 compared to those of end-members (dotted polygons from Fig. 3). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of calculated diets (\square) were obtained by subtracting trophic enrichment (dashed lines) of 1 and 3.4‰ respectively from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both species. POM: particulate organic matter.

(verified using the Shapiro–Wilk test and the F test, respectively).

3. Results

3.1. Seasonal variations of suspension-feeder isotopic compositions

$\delta^{13}\text{C}$ values for *C. fornicata* were less variable (range = -17.9‰ to -17.1‰ , p (KW) = 0.318, CV = 1.1) than for *C. gigas* over the sampling period (range = -18.7‰ to -17.8‰ , p (KW) ≤ 0.001 , CV = 1.7), and were ^{13}C -enriched by 0.5‰ to 1.6‰ (Fig. 2). Significant differences were observed in $\delta^{13}\text{C}$ values between the two species for 13 of the 18 months of the study, predominantly in winter and spring (Fig. 2); Pacific oysters were thus ^{13}C -depleted compared to common Atlantic slippersnails.

The seasonal variations in $\delta^{15}\text{N}$ values were similar to those for $\delta^{13}\text{C}$ (Fig. 2). As was the case for the $\delta^{13}\text{C}$, the *C. fornicata* values were characterized by a low-amplitude seasonal variation (range = 8.5 to 10‰, p (KW) ≤ 0.001 , CV = 3.8), whereas those of *C. gigas* presented much more marked seasonal variations (range = 8 to 11.1‰, p (KW) ≤ 0.001 , CV = 9.5). It should be noted that $\delta^{15}\text{N}$ values are known to be generally more variable in nature than those of $\delta^{13}\text{C}$ (Riera et al., 1999). The amplitude of these variations nevertheless produced an inversion of the common Atlantic slippersnail and Pacific oyster curves between March and April of both

2003 and 2004, with an abrupt oyster $\delta^{15}\text{N}$ decrease of approx. 2–3‰, followed by a steady increase until December. In spring and summer, Pacific oysters were thus ^{15}N -depleted, compared to winter values. Significant differences were found between $\delta^{15}\text{N}$ deviations of the two species for 10 of the 18 months sampled (Fig. 2): Pacific oysters were significantly ^{15}N -enriched relative to common Atlantic slippersnails from January to March and ^{15}N -depleted from April to June–July.

3.2. Phytoplankton observations

Essential indices of food resource availability were monitored over the sampling period. Phytoplankton concentrations were low in January–February 2003, and from October 2003 to February 2004 (Fig. 3a). A major bloom occurred in March 2003 and 2004, corresponding to predominantly higher chlorophyll *a* concentrations, and persisted into summer (Fig. 3b). This bloom matched the spring ^{13}C and ^{15}N depletion observed in oyster isotopic compositions. A third chlorophyll *a* peak, recorded in September–October 2003, was not associated with an increase in phytoplankton concentration, but was concomitant with high phaeopigment concentrations (Fig. 3c). The REPHY data showed more phaeopigments in Bourgneuf Bay from the beginning of the study to April 2003, and from the late summer 2003 to May 2004. Higher phaeopigment concentrations seemed to correspond with ^{15}N enriched oyster.

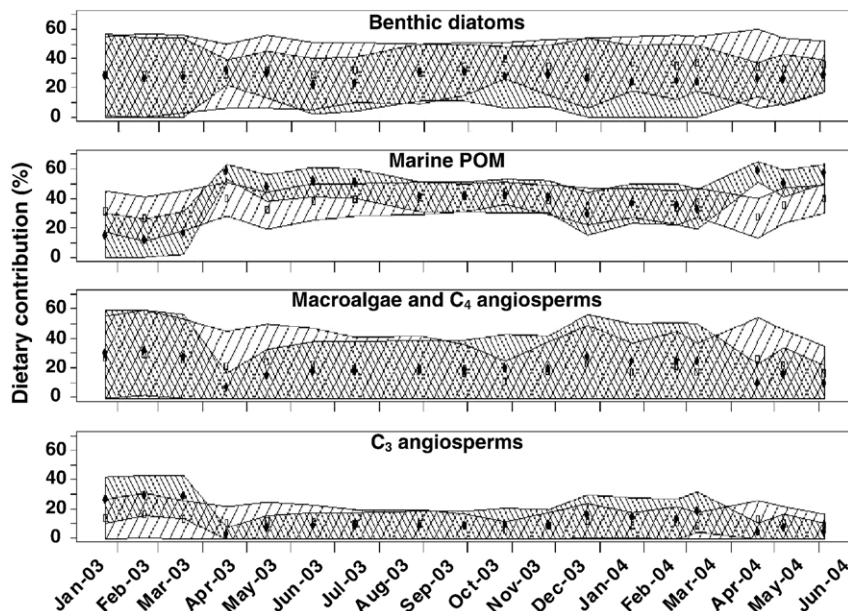


Fig. 6. Seasonal variations of feasible end-member contributions (1–99 percentile ranges and means) to the diets of *Crepidula fornicata* (▨) and *Crassostrea gigas* (▩) calculated using the IsoSource model. POM: particulate organic matter.

3.3. Seasonal variations of dietary contributions

The dominant dietary sources for *C. fornicata* and *C. gigas* have been documented previously: macroalgae, C₄ angiosperms such as *Spartina* sp., benthic diatoms, and suspended POM. A dual plot of all source and consumer deviations measured over the survey placed the calculated diets at the center of a polygon bounded by these four end-members (Fig. 4). Slippersnail and oyster diets were close to macrophytes throughout the year.

As the spring inversion of oyster isotopic compositions was contemporaneous with indices of phytoplankton abundance, we plotted the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ of sources and calculated diets in March (pre-inversion) and April (inversion), for both 2003 and 2004, to determine whether the calculated oyster diet was closer to POM in spring (Fig. 4). The results of Fig. 5 confirm this explanation, mainly with respect to nitrogen, placing the calculated diet closer to POM and further from macrophytes in April compared to March. The changes in the indiscriminate suspension-feeding slippersnail calculated diet were much less marked in this interval.

Variations in the relative biomass contributions of the four dietary end-members are presented in Fig. 6, calculated using the IsoSource model (Phillips and Gregg, 2003). Benthic diatom contribution was constant and similar for both species, over the course of the study, with $27 \pm 3\%$ for oyster and $32 \pm 3\%$ (means \pm SDs) for slippersnails. In contrast, the two species showed marked differences in the contributions of the other three end-members. These contributions were stable in the slippersnail diet over the course of the study, with means \pm SD of $36 \pm 5\%$, $21 \pm 4\%$ and $10 \pm 2\%$ for marine POM, macroalgae-C₄ angiosperms and C₃ angiosperms, respectively. Oyster contributions were much more variable, notably with a much greater transitory contribution of marine POM (i.e. largely phytoplankton): approximately 30% more after the spring inversion observed in both 2003 and 2004. Consumption of macrophyte detritus (macroalgae-C₄ angiosperms and C₃ angiosperms) by oysters increased concomitantly by approximately the same proportion in both years. Dietary contributions of all end-members were much less variable in oysters throughout the rest of the year.

4. Discussion

Given that animals which have similar diets must present similar carbon and nitrogen isotope deviations (e.g. Fry et al., 1987; Riera et al., 2002), the comparative analysis of isotopic deviations of *C. fornicata* and *C. gigas* indicate divergent diets from winter until early

summer, and similar diets in late summer to autumn. Trophic niche overlap is thus partial from January to June–July, and total from July–August to November. Although *C. fornicata* and *C. gigas* exploit the same end-members in Bourgneuf Bay throughout the year (Decottignies et al., in press), the data of the present study suggest that they ingest and assimilate the end-members in different proportions, for significant durations throughout the year. The mean difference in phytoplankton proportions consumed by common Atlantic slippersnails and Pacific oysters thus reached 15% over a period of 7 months, in both 2003 and 2004.

The seasonal differences in isotopic deviations between the two species were due to the considerable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations of oysters. The major ^{15}N -depletion of Pacific oysters which occurred between March and April coincided with a previously documented microalgal bloom (Gohin et al., 2003), confirmed by our phytoplanktonic data, and with microphytobenthic blooms on mudflats (Guarini et al., 1998; Hamels et al., 1998; Méléder et al., 2005). Although previous studies have inferred a greater exploitation of microalgal sources during blooms (Page and Lastra, 2003), or the major exploitation of the predominant carbon sources available (Sarà et al., 2003), a fundamental difference in suspension-feeding mechanisms may explain the difference in degree of microalgal exploitation by *C. gigas* and *C. fornicata*. The more pronounced ^{13}C and ^{15}N -depletions in oysters, compared to slippersnails, suggest a selective shift from the more refractory macrophyte detritus (Newell and Langdon, 1986; Crosby et al., 1989) to microalgae during the bloom, via the qualitative selection capability of Pacific oysters (Barillé et al., 1997; Cognie et al., 2003). This selective shift produced up to a 30% decrease in macrophyte contribution to oyster diet. In contrast, common Atlantic slippersnails are indiscriminate suspension-feeders (Beninger et al., in press); the fluctuations of their isotopic deviations therefore reflected the natural

Table 1

Interpretation of trophic relationships between *Crepidula fornicata*, *Crassostrea gigas* and dominant resources, based on stable isotopic compositions and resource availability

Season	Summer/ autumn	Winter	Spring
Difference in isotopic compositions	No	Yes	Yes
Microalgal resource limitation	No	Yes	Yes
Dominant resource	?	Detritus	Microalgae
Oyster selection activated	No	Detritus +	Microalgae +
Degree of overlap	High	Reduced	Reduced
Competition	No	Probable	Probable

variations of source relative abundances in the water column.

A similar argument can be made concerning the higher $\delta^{15}\text{N}$ of Pacific oysters during the winter months, both relative to the rest of the year, and in comparison with common Atlantic slippersnails. Assuming that the slippersnail isotopic deviations reflect the source availability, this finding in oysters can only be explained by increased ingestion of macrophyte detritus, most probably mediated by qualitative selection of the best-quality food source predominantly available at this time. Although to our knowledge, comparisons of the nutritional values (in terms of energetic contribution and recommended daily intake) of the various food sources naturally available to bivalves are totally lacking, the well-documented growth data for oysters in Bourgneuf Bay (REMORA, 2003) strongly argues for energetic limitation. Several lines of evidence indicate that this limitation is a consequence of an exceeded carrying capacity of Bourgneuf Bay (Barillé-Boyer et al., 1997), a situation likely to occur with increasing frequency in bivalve-farming ecosystems. It is thus likely that the year-round proximity of both species to the detrital component reflects the dominant POM in the case of the indiscriminate suspension-feeding slippersnail, and reflects lack of better quality and quantity in the case of the facultatively selective suspension-feeding oyster. Under conditions of food limitation, as here in winter and spring, trophic competition between slippersnails and oysters can be inferred. This competition would take place at a time of year when food resources are most scarce and most refractory, while at the same time energetic demands of oysters are high, due to the initiation of gametogenesis. The probable pattern of trophic relationships between these two suspension-feeders and the dominant food sources is summarized in Table 1.

The results of the present study suggest that the year-round pattern of trophic resource exploitation by suspension-feeding molluscs depends in part upon their capacity for qualitative selection. To our knowledge, this dimension of aquatic ecology has not previously been explored; further research is thus eminently necessary.

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