Benthic community respiration in areas impacted by the invasive mollusk *Crepidula fornicata*

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ABSTRACT: The American slipper limpet *Crepidula fornicata* L. has been an invasive species in European bays and estuaries since the 1950s and can reach densities up to several thousands of individuals m^{-2}. The objective of this study was to estimate the impact of *C. fornicata* on benthic community metabolism by comparing 2 contrasting sites with high (>1000 ind. m^{-2}) and low (<200 ind. m^{-2}) densities in the Bay of Brest (Brittany, France). Measurements of dissolved oxygen (DO) and dissolved inorganic carbon (DIC) fluxes at the water–sediment interface were investigated using benthic chambers. Community respiration (CR) was 1.5- to 3-fold higher at the station with high densities, where it varied from 1.5 mmol C m^{-2} h^{-1} in winter to 5.9 mmol C m^{-2} h^{-1} in summer, and, considering *C. fornicata* biomass, from 0.7 mmol C g^{-1} dry wt h^{-1} in winter to 3.3 mmol C g^{-1} dry wt h^{-1} in summer. CR was mainly controlled by *C. fornicata* biomass, temperature, and chl *a* concentration in the water column. Community respiratory quotients (CRQ = $|CR_{DIC} / CR_{DO}|$) were 0.74 in winter–spring and 1.38 in summer–autumn. Annual CR averaged 440 g C m^{-2} yr^{-1} at the highly colonized station, and 180 g C m^{-2} yr^{-1} at the station displaying low density of *C. fornicata*. The estimated annual CR for an average density of 260 ind. m^{-2} in the whole Bay of Brest was 220 g C m^{-2} yr^{-1}, which was higher than the carbon production of the overlying phytoplankton and microphytobenthos in the bay. *C. fornicata* is thus considered a source of carbon influencing partial pressure of CO_2 in seawater and favoring CO_2 effluxes to the atmosphere.

KEY WORDS: Benthic community respiration · Carbon cycling · Invasive species · *Crepidula fornicata* · Water–sediment interface

INTRODUCTION

The ecological impact of aquatic invasive species is a growing concern for coastal zone management and conservation (Grosholz 2002). The multiple ecological effects of invaders and their impact on native species populations and related ecosystems have been widely documented (Mack et al. 2000, Stachowicz & Byrnes 2006). At the ecosystem level, invasive species influence the processes determining carbon and nutrient cycling (Arnott & Vanni 1996, Ragueneau et al. 2002, Martin et al. 2006). In aquatic environments, mollusks such as *Dreissena polymorpha*, *Ruditapes philippinarum*, *Potamocorbula amurensis*, and *Crepidula fornicata* are among the most common invaders (Carlton et al. 1990, Mills et al. 1993, Blanchard 1997, Chauvaud et al. 2003). These species are very active suspension feeders, and their dense assemblages may exert a strong influence on suspended particulate matter (Dame 1996). The feeding activity of filter feeders results in the packaging of suspended material into feces and pseudofeces that settle to the bottom, diverting primary production and energy flow from planktonic to benthic food webs and increasing the release of dissolved end products of organic matter mineralization from the bottom (Arnott & Vanni 1996).

In addition to stimulating benthic bacterial respiration through biodeposition, suspension feeders also release carbon through their own metabolism (Chauvaud et al. 2003, Martin et al. 2006). In shallow coastal waters, benthic communities dominated by dense populations of suspension feeders are important zones for carbon cycling and may dominate ecosystem processes and metabolism (Middelburg et al. 2005).

The American slipper limpet *Crepidula fornicata* L. was mainly introduced in Europe in the late 1940s early 1950s and has rapidly invaded coastal waters from the Mediterranean to the Baltic Sea. At present, *C. fornicata* proliferates in bays and estuaries, reaching several thousands of individuals m^{-2} (Blanchard 1997). In the Bay of Brest, France, *C. fornicata* colonizes more than half of the benthic surface area (Guérin 2004) and induces both economic and ecological consequences through disturbance of mollusk cultures and fisheries, and shifts in benthic community species composition and trophic structure (Chauvaud et al. 2000, Thouzeau et al. 2000). In affected areas, the high respiration rate of *C. fornicata* enhances the partial pressure of CO_2 (pCO_2) in seawater and subsequent CO_2 effluxes to the atmosphere (Martin et al. 2006). *C. fornicata* also influences carbon fluxes in the benthic community by stimulating the bacterial decomposition processes through its high biodeposition (Chauvaud et al. 2000, Ragueneau et al. 2002, 2005). Increased benthic respiration and mineralization can decrease dissolved oxygen (DO) concentration, inducing shifts to hypoxic conditions in sediments (Stenton-Dozey et al. 2001). However, the impact of *C. fornicata* on DO and carbon fluxes has never been assessed at the community level. The objective of this study was to estimate the effect of the mollusk invasion on community metabolism by comparison of oxygen and carbon fluxes at 2 stations with contrasting densities of *C. fornicata*.

MATERIALS AND METHODS

Site description. The Bay of Brest is a shallow semi-enclosed marine ecosystem of 180 km^2 located at the extreme west of Brittany, France (Fig. 1). The hydrology of the bay is controlled by tidal forcing and is influenced by the moderate input of 2 rivers (Elorn and Aulne). The bay is a shallow basin (50% of its surface is <5 m in depth below Chart Datum) with more than half of its benthic surface colonized by *Crepidula fornicata* (Guérin 2004). The experiments were
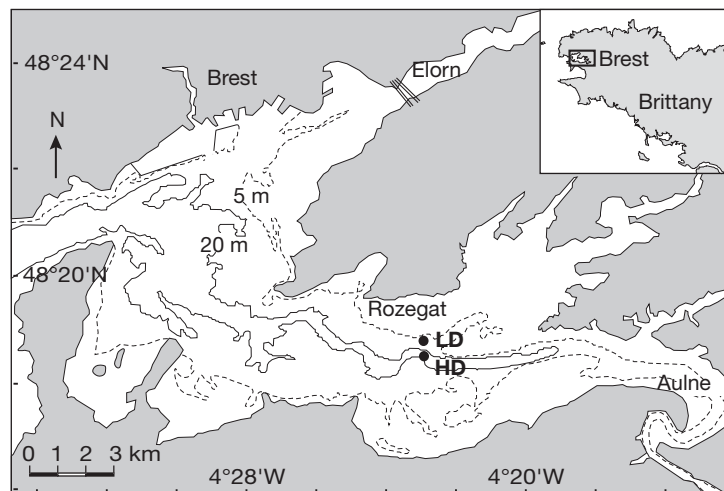

Fig. 1. Locations of the experimental stations (HD, high *Crepidula fornicata* density; LD, low *C. fornicata* density) at the Rozegat site in the Bay of Brest, France

performed at the Rozegat site, at 2 stations with contrasting *C. fornicata* densities: >1000 ind. m^{-2} at Stn HD and <200 ind. m^{-2} at Stn LD. The 2 stations were situated 300 m apart. The field experiments took place between May 2000 and September 2004 (Table 1) and were carried out from the RV 'Côtes de la Manche'. Average water depth was 20 m at Stn HD and 10 m at Stn LD. Temperature, chlorophyll *a* (chl *a*), and DO concentrations in surface waters were provided by the automated MAREL Iroise Station (IUEM-UBO, Observatoire du Domaine Côtier) located in the west of the Bay of Brest. During the sampling period, temperature varied from 8.4°C in winter to 18.7°C in summer, chl *a* concentration varied from minima (0.3 to 0.5 µg l^{-1}) in January to maxima (2.7 to 6.4 µg l^{-1}) in April-May, and DO concentration varied from minima (5.1 to 5.3 ml l^{-1}) between August and October to maxima (6.9 to 7.6 ml l^{-1}) between March and May in surface waters (Fig. 2).

Field measurements. *In situ* measurements of fluxes at the water–sediment interface were performed according to Martin et al. (2005). Three replicate opaque benthic chambers were deployed, covering an area of 0.2 m^2 and

Table 1. Experimental periods and number of incubations at Stns HD and LD

Season	Date	HD	LD
Winter	February 2004	9	3
Spring	May to June 2000, May 2001, May 2002	22	16
Summer	September 2004	6	6
Autumn	October 2001, October 2002	12	12

incubating a known volume (~60 l) of bottom water. A series of incubations was carried out for 120 to 240 min. DO concentration (mg l^{-1}), salinity (in practical salinity units, PSU), temperature (°C), and depth (m) were recorded every minute inside the chambers with YSI 6920 probes. Water samples were collected from the benthic chambers using 450 ml syringes, for pH and total alkalinity (TA) at the beginning and end of the incubations. Water samples were passed through GF/F filters and poisoned with mercuric chloride (DOE 1994). Fauna enclosed in the chambers was collected by SCUBA divers using an airlift suction sampler at the end of the incubations. Three samples of surface-sediment were collected with cores at Stns LD and HD and frozen for subsequent organic content analysis in May 2000, May 2001, and October 2001.

Sample processing. The pH (in total scale) was measured immediately on board using a pH meter (PHM 240, Radiometer) calibrated against buffer solutions (TRIS/HCl and 2-aminopyridine/HCl) in seawater (DOE 1994). TA was measured on 50 ml subsamples using the automatic potentiometric method, with Gran titration (Titrilab TIM 865, Radiometer). The concentration of total dissolved inorganic carbon (DIC) was calculated from pH, TA, temperature, and salinity (Lewis & Wallace 1998).

Crepidula fornicata individuals were sorted and counted. Shell length was measured (±0.01 mm), and total dry weight (DW; ±0.001 g) of samples (shells + soft body) was determined after drying at 60°C for 72 h. Population structure was established through size frequency histograms (1 mm intervals). Sediment samples for organic content analysis were dried at 60°C, weighed, and reweighed after combustion for 4 h at 450°C.

Data treatment. DO, DIC, and TA fluxes were calculated by the difference between the initial and final concentrations in the enclosures:

$$F_x = \frac{\Delta x \times v}{s \times \Delta t} \qquad (1)$$

where F_x represents community fluxes of x = DO, DIC (mmol m^{-2} h^{-1}), or TA (mequiv. m^{-2} h^{-1}); Δx is the change in the concentration of x = DO, DIC (mmol l^{-1}), or TA (mequiv. l^{-1}) during the incubation; v is the chamber volume (l); s is the enclosed surface area (m^2); and Δt is the incubation time (h).

Community respiration (CR, mmol m^{-2} h^{-1}) was estimated from DO consumption (CR$_{DO}$ = F_{DO}), including both aerobic respiration and oxidation of end products of anaerobic metabolism. CR was also measured from DIC release (CR$_{DIC}$), representing all respiration pathways (aerobic respiration, denitrification, and reduction of manganese, iron, and sulfate; Middelburg et al. 2005). In communities dominated by calcifying

organisms, CR$_{DIC}$ is usually estimated by subtracting the change in DIC resulting from community net calcification (Ca^{2+} + 2HCO$_3^-$ → CaCO$_3$ + CO$_2$ + H$_2$O; ΔTA = −2 equiv.; Gattuso et al. 1999) from F_{DIC} using the alkalinity anomaly technique (Chisholm & Gattuso 1991):

$$CR_{DIC} = F_{DIC} - {}^1\!/_2\, F_{TA} \qquad (2)$$

However, ammonification (NO$_3^-$ + 2 H$^+$ + H$_2$O → NH$_4^+$ + 2 O$_2$; ΔTA = +2 equiv.) and sulfate reduction (SO$_4^{2-}$ + 2 H$^+$ → H$_2$S + 2O$_2$; ΔTA = +2 equiv.; Gattuso et al. 1999, Middelburg et al. 2005) may significantly alter F_{TA} in organic matter enriched systems, and, in that case, the simple correction of F_{DIC} by F_{TA} cannot be applied. In our study, CR$_{DIC}$ was calculated from F_{DIC} corrected for calcification effects:

$$CR_{DIC} = F_{DIC} - {}^1\!/_2\, F_{TAcalc} \qquad (3)$$

where F_{TAcalc} is the change in TA from *Crepidula fornicata* calcification (mequiv. m^{-2} h^{-1}). Indeed, *C. fornicata* is the predominant calcifying organism in the
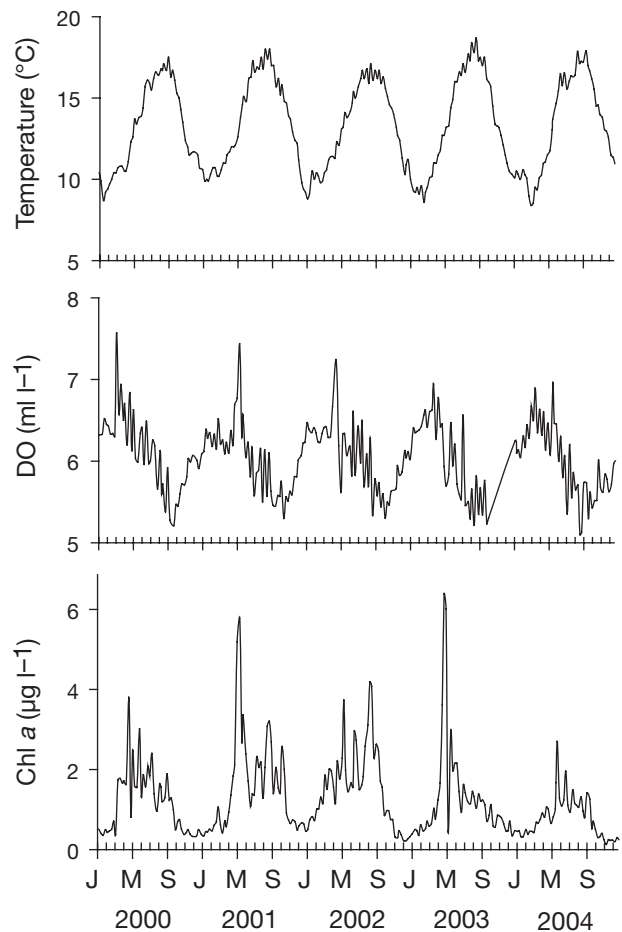

Fig. 2. Evolution of mean values of surface-water temperature, dissolved oxygen (DO), and chl *a* concentrations recorded at Stn MAREL Iroise for the period from 2000 to 2004 (J: January, M: May, S: September)

community, representing more than 95% of the total biomass of calcifying organisms (S. Martin unpubl. data). The rate of calcification by *C. fornicata* was estimated seasonally from size frequency distributions and density measured during the experiments, and from seasonal allometric relationships between shell length and body weight and between body weight and calcification rates reported by Martin et al. (2006). Change in TA from $CaCO_3$ dissolution was neglected, as the dissolution rate of accumulated dead *C. fornicata* shells in the community was estimated to be <0.1 µequiv. d^{-1} g^{-1} DW of shell (S. Martin unpubl. data). Change in TA due to processes other than calcification was expressed as $F'_{TA} = F_{TA} - F_{TAcalc}$.

A community respiratory quotient (CRQ = $|CR_{DIC} / CR_{DO}|$) was established for each season. As DIC release and DO consumption are both affected by natural variability and measurement errors, the community metabolic quotients were calculated by means of functional regressions (Ricker 1973).

The effect of season and station was tested using 1- and 2-way analyses of variance (ANOVA) followed by Newman-Keuls tests. Normal distribution (Shapiro-Wilks test) and equality of variance (Levene test) were verified prior to analysis. When required, data were log-transformed. The annual estimates of CR at Stns HD and LD were calculated by summing mean seasonal CR. CR_{DO} and CR_{DIC} (mmol m^{-2} h^{-1}) were related to *Crepidula fornicata* total biomass (g DW m^{-2}) using linear relationships (CR = $a \times$ DW + b) where a and b are coefficients. Covariance analyses (ANCOVAs) were performed to test heterogeneity of a and b coefficients among seasons. Pairwise ANCOVAs were conducted to test significant differences between pairs of seasons. Multiple regression analyses were used to test relationships between CR and *C. fornicata* biomass, bottom-water temperature, and surface-water chl *a* concentration. Data were checked for normality and equal variances. To extrapolate our data to carbon fluxes in the whole ecosystem of the Bay of Brest, we considered the average density of *C. fornicata* over the whole area (260 ind. m^{-2}) corresponding to a total bio-

mass of 668 g DW m^{-2} (Guérin 2004, Martin et al. 2006). To estimate the potential impact of *C. fornicata* proliferation from pre-invasion (0 ind. m^{-2}) to high proliferation patterns, we also considered the mean density of highly colonized areas (1700 ind. m^{-2}), corresponding to 4368 g DW m^{-2} (Ragueneau et al. 2002, Martin et al. 2006). In this case, the daily estimates of CR were calculated monthly from multiple regressions, and the annual estimates of CR were calculated by summing estimates of monthly CR.

RESULTS

Environmental parameters and population structure of *Crepidula fornicata*

During the experiments, bottom-water temperature, salinity, and DO concentration measured inside the benthic chambers at the beginning of the incubations were similar for the 2 Rozegat stations (Stns HD and LD). Mean (±SD) seasonal bottom-water temperature, salinity, DO concentration, and surface-water chl *a* concentration are presented in Table 2. Sediment comprised 9.3 ± 2.2% of organic matter at Stn HD and 5.9 ± 1.5% at Stn LD. The average density of *Crepidula fornicata* was 1224 ± 239 ind. m^{-2} at Stn HD and 62 ± 77 ind. m^{-2} at Stn LD, corresponding to a total biomass of 2840 ± 553 and 105 ± 46 g DW m^{-2}, respectively. The Stn HD size frequency distribution of the *C. fornicata* population varied seasonally (Fig. 3). The proportion of small (<20 mm shell length) *C. fornicata* at Stn HD was highest in summer (25%) and lowest in spring (12%); accordingly, the mean shell length was minimal in summer (27.4 ± 9.3 mm) and maximal in spring (31.1 ± 7.9 mm). The relative frequency of intermediate-sized individuals (20 to 40 mm) varied from 70% in winter to 82% in autumn, and the proportion of large individuals (>40 mm) varied from 5% in summer–autumn to 14% in winter. The proportion of small *C. fornicata* at Stn LD in summer was 80%, while the proportions of intermediate and large individuals were 16 and 4%,

Table 2. Mean ± SD seasonal temperature, salinity, and dissolved oxygen (DO) concentration in bottom waters, chl *a* concentration in surface waters at Stn MAREL Iroise, and *Crepidula fornicata* density and biomass (DW: dry weight) measured at Stns HD and LD during the chamber experiments

Season	Temperature (°C)	Salinity (PSU)	DO (mg l^{-1})	Chl *a* (µg l^{-1})	Mean density (ind. m^{-2})		Mean biomass (g DW m^{-2})	
					HD	LD	HD	LD
Winter	8.7 ± 0.1	34.5 ± 0.1	9.7 ± 0.3	0.5 ± 0.0	828 ± 142	17 ± 18	1825 ± 340	47 ± 46
Spring	13.7 ± 0.4	33.8 ± 0.4	9.1 ± 1.1	3.4 ± 1.8	1351 ± 367	30 ± 67	3748 ± 741	117 ± 264
Summer	17.5 ± 0.1	36.0 ± 0.0	8.4 ± 0.5	1.4 ± 0.0	1007 ± 211	177 ± 133	1839 ± 321	158 ± 180
Autumn	14.8 ± 0.3	34.9 ± 0.1	8.0 ± 0.2	2.0 ± 0.8	1790 ± 309	23 ± 37	3948 ± 811	98 ± 162

respectively. The mean shell length at Stn LD in summer was thus very low (11.7 ± 13.1 mm). The size frequency distributions of the *C. fornicata* population at Stn LD in winter, spring, and autumn were not assessed because of the low numbers of collected individuals (<30 ind. m^{-2}).

Community respiration

CR was significantly affected by station (2-way ANOVAs, F = 181.04, p < 0.001 and F = 106.01, p < 0.001, for DO and DIC, respectively), being 2-, to 4-fold higher at Stn HD than at Stn LD, and season (2-way ANOVAs, F = 17.48, p < 0.001 and F = 22.04, p < 0.001, for DO and DIC, respectively; Fig. 4). The significant interaction between season and station (p < 0.001) showed a different seasonal response depending on the station. At Stn HD, CR varied seasonally (1-way ANOVAs, F = 21.52, p < 0.001 and F = 38.47, p < 0.001, for DO and DIC, respectively) from –1.51 ± 0.14 (mean ± SD) mmol DO m^{-2} h^{-1} in winter to –4.77 ± 1.12 mmol DO m^{-2} h^{-1} in spring and summer, and from 1.47 ± 0.43 mmol DIC m^{-2} h^{-1} in winter to 5.86 ± 0.67 mmol DIC m^{-2} h^{-1} in summer. At Stn LD, CR$_{DO}$ varied significantly according to season (1-way ANOVA, F = 7.16, p = 0.001), with the highest value in summer (–1.63 ± 0.34 mmol DO m^{-2} h^{-1}), and the lowest between autumn and spring (–1.00 ± 0.37 mmol DO m^{-2} h^{-1}), while CR$_{DIC}$ did not differ significantly between seasons, with an overall mean of 1.77 ± 0.39 mmol DIC m^{-2} h^{-1}.

CR was significantly related to *Crepidula fornicata* biomass, except for DIC fluxes in winter and autumn (Table 3). The rise in CR per biomass unit (*a* coefficient) increased by a factor of 3 between autumn–winter and spring–summer for DO fluxes and between spring and summer for DIC fluxes. CR without *C. fornicata* (*b* coefficient) varied from autumn–winter to summer by a factor of 2 for DO fluxes, but did not differ significantly for DIC fluxes. CR per biomass unit (Fig. 5) varied significantly among seasons (1-way ANOVAs, F = 26.29, p < 0.001 and F = 82.45, p < 0.001 for DO and DIC, respectively) from autumn–winter (–0.88 mmol DO g^{-1} DW h^{-1} and 0.83 mmol DIC g^{-1} DW h^{-1}) to summer (–2.59 mmol DO g^{-1} DW h^{-1} and 3.27 mmol DIC g^{-1} DW h^{-1}).

CR was also correlated with temperature (r = 0.75, p < 0.001 and r = 0.85, p < 0.001 for DO and DIC, respectively) and with chl *a* for DO fluxes (r = 0.83, p < 0.001), but not for DIC fluxes (r = 0.23, p > 0.05). Standard multiple regression analysis showed that temperature (*T*), *Crepidula fornicata* biomass (DW), and chl *a* concentration controlled 73% of CR$_{DO}$ data variability, while *T* and DW controlled 67% of CR$_{DIC}$ data variability:
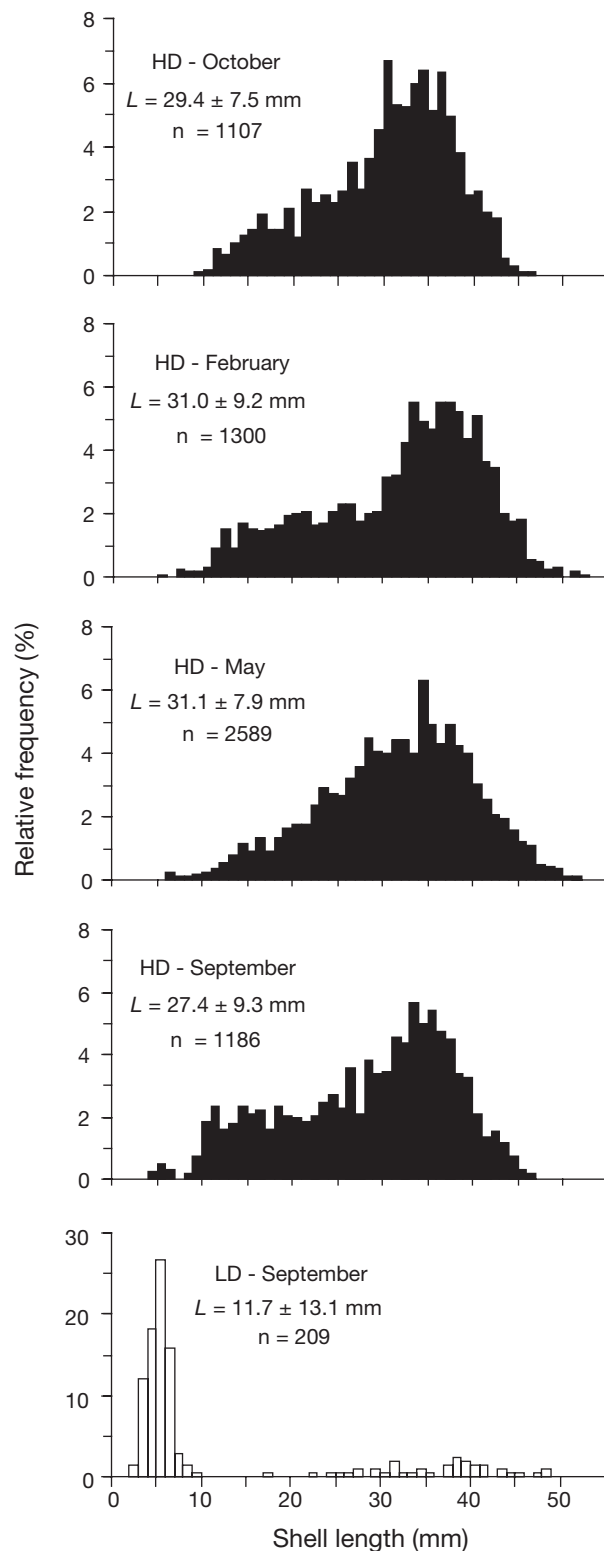

Fig. 3. *Crepidula fornicata.* Seasonal size frequency distributions of individuals at Stn HD (data from May 2000 and 2001, October 2002, February 2004, and September 2004) and at Stn LD in summer (data from September 2004). *L*: mean (±SD) shell length; n: number of observations
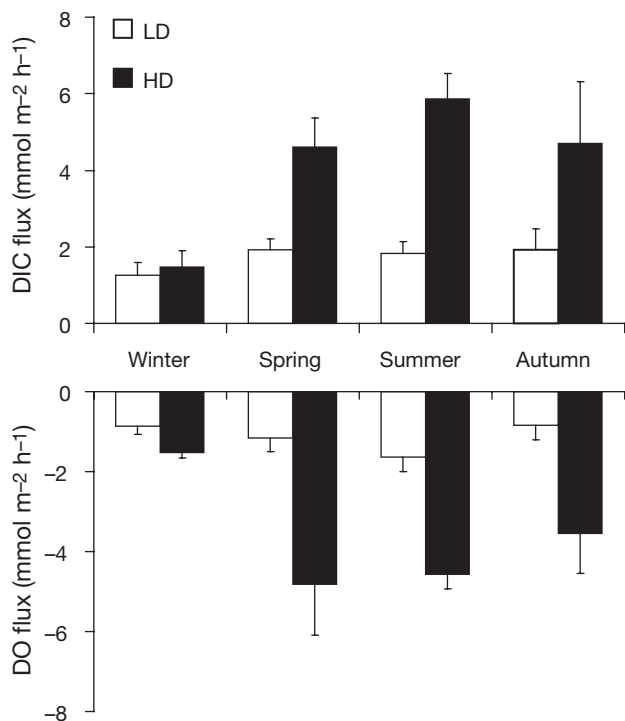
Fig. 4. Seasonal community respiration (mean ± SD) expressed per surface unit in dissolved inorganic carbon (DIC) release (CR_{DIC}) and dissolved oxygen (DO) consumption (CR_{DO}) at Stns HD and LD

$$CR_{DO} = 0.18\ T + 0.88 \times 10^{-3}\ DW + 0.08\ \text{chl}\ a - 1.57$$
$$(F_{3,\,68} = 60.42,\ p < 0.001)$$

$$CR_{DIC} = 0.28\ T + 0.79 \times 10^{-3}\ DW - 2.16$$
$$(F_{2,\,39} = 39.50,\ p < 0.001)$$

In the calculation of CR_{DIC} from F_{DIC} and F_{TAcalc} (Table 4), we considered that F_{TAcalc} was negligible in winter, spring, and autumn at LD because of the low numbers of *Crepidula fornicata*. F_{TA} was positive, except in spring at HD. F'_{TA} at Stn HD resulting from the difference between F_{TA} and F_{TAcalc} was lowest in winter and spring and highest in summer and autumn, being up to 4-fold higher than at Stn LD.

Community respiratory quotients

CRQ and intercepts did not differ significantly between winter and spring (*Z*-test, $Z = 0.34$, $p = 0.63$ and $Z = 0.20$, $p = 0.84$, respectively) and between summer and autumn (*Z*-test, $Z = 0.33$, $p = 0.74$ and $Z = 0.77$, $p = 0.44$, respectively). The common CRQ in winter-spring was 0.74 ± 0.24 (mean ± SD) and was significantly < 1 (*Z*-test, $Z = 5.27$, $p < 0.001$). The common intercept was 0.49 ± 0.15 mmol m^{-2} h^{-1} and was signif-

Table 3. Parameter values (SE) calculated by linear regressions of community respiration (CR_{DO} or CR_{DIC}; mmol DO or DIC m^{-2} h^{-1}) vs. total biomass (g DW m^{-2}), expressed as CR_{DO} (or CR_{DIC}) = $a \times 10^{-3} \times DW + b$. Superscripts indicate significant differences between seasons after pairwise comparisons (ANCOVAs; $p < 0.05$); nd: no difference; n: number of observations, r^2: proportion of variance explained by the regression, p: p-value

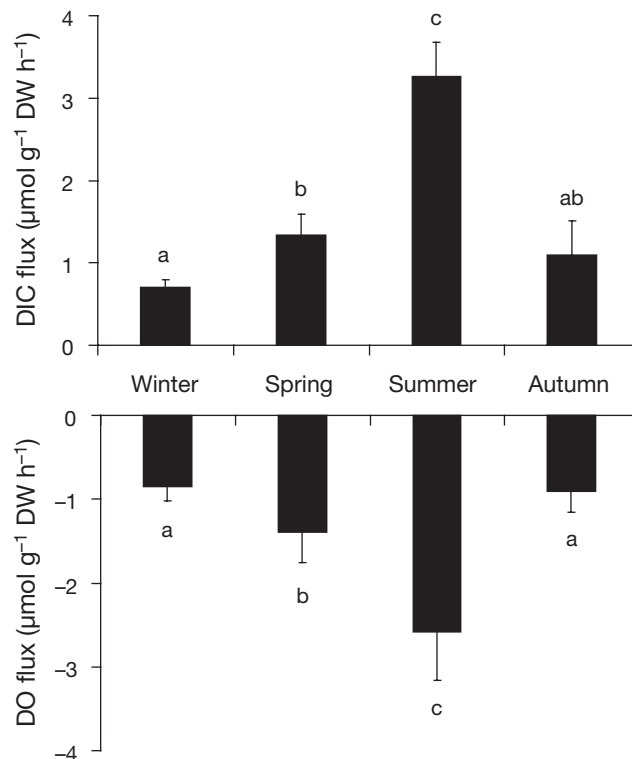| Season	a	b	n	r^2	p
CR_{DO}					
Winter	−0.34[a] (0.06)	−0.88[a] (0.09)	11	0.79	<0.001
Spring	−1.04[b] (0.10)	−1.10[b] (0.27)	31	0.80	<0.001
Summer	−1.61[b] (0.21)	−1.49[c] (0.26)	11	0.87	<0.001
Autumn	−0.68[a] (0.07)	−0.82[a] (0.19)	18	0.83	<0.001
CR_{DIC}					
Winter	0.07 (0.15)	1.33 (0.24)	11	0.02	0.657
Spring	0.85[a] (0.14)	1.57[nd] (0.37)	14	0.75	<0.001
Summer	2.29[b] (0.18)	1.57[nd] (0.23)	11	0.97	<0.001
Autumn	0.62 (0.31)	1.97 (1.04)	5	0.57	0.140

Fig. 5. Seasonal community respiration (mean ± SD) expressed per biomass unit in DIC release (CR_{DIC}) and DO consumption (CR_{DO}) at Stn HD. Different letters on bars indicate significant differences among means (Newman-Keuls test, $p < 0.05$). DW: dry weight

icantly > 0 (*Z*-test, $Z = 3.31$, $p < 0.001$). The common functional regression explained 90% of data variability. The common CRQ in summer–autumn was 1.38 ± 0.56 and was significantly > 1 (*Z*-test, $Z = 2.75$, $p = 0.01$). The common intercept was -0.16 ± 0.08 mmol

Table 4. Mean ± SD seasonal community DIC fluxes (F_{DIC}, mmol m^{-2} h^{-1}), calculated community respiration (CR$_{DIC}$, mmol m^{-2} h^{-1}), community total alkalinity (TA) fluxes (F_{TA}, mequiv. m^{-2} h^{-1}), ΔTA from *Crepidula fornicata* CaCO$_3$ precipitation (F_{TAcalc}, mequiv. m^{-2} h^{-1}), and ΔTA due to processes other than calcification (F'_{TA}, mequiv. m^{-2} h^{-1}). ΔTA from *C. fornicata* calcification was estimated from seasonal size frequency distributions and densities measured seasonally at HD and in summer at LD, and from seasonal allometric relationships for *C. fornicata* calcification reported by Martin et al. (2006)

Season	F_{DIC}	CR$_{DIC}$	F_{TA}	F_{TAcalc}	F'_{TA}
HD					
Winter	1.56 ± 0.43	1.47 ± 0.43	0.85 ± 0.32	0.18 ± 0.03	0.67 ± 0.32
Spring	4.14 ± 0.76	4.60 ± 0.78	−0.32 ± 0.61	−0.92 ± 0.11	0.59 ± 0.63
Summer	4.78 ± 0.47	5.86 ± 0.67	1.34 ± 0.38	−2.16 ± 0.51	3.50 ± 0.74
Autumn	4.08 ± 1.62	4.69 ± 1.63	1.59 ± 0.66	−1.21 ± 0.06	2.80 ± 0.68
LD					
Winter	1.27 ± 0.31	1.27 ± 0.31	0.97 ± 0.27	0	0.97 ± 0.27
Spring	1.93 ± 0.29	1.93 ± 0.29	0.76 ± 0.41	0	0.76 ± 0.41
Summer	1.81 ± 0.30	1.83 ± 0.30	0.90 ± 0.59	−0.04 ± 0.03	0.94 ± 0.58
Autumn	1.92 ± 0.56	1.92 ± 0.56	1.25 ± 1.39	0	1.25 ± 0.97

m^{-2} h^{-1} and did not differ significantly from zero (*Z*-test, $Z = 0.41$, p = 0.69). The common functional regression explained 87% of data variability.

Carbon budget

Daily CR measured during our experiments varied seasonally from 0.42 ± 0.12 (mean ± SD) to 1.69 ± 0.19 g C m^{-2} d^{-1} at Stn HD, and from 0.37 ± 0.09 to 0.56 ± 0.08 g C m^{-2} d^{-1} at Stn LD. Annual CR was estimated to be 437 ± 92 g C m^{-2} yr^{-1} at Stn HD and 183 ± 38 g C m^{-2} yr^{-1} at Stn LD. Estimated daily CR calculated from multiple linear regression ranged from 1.17 to 1.76 g C m^{-2} d^{-1} for a *Crepidula fornicata* density of 1700 ind. m^{-2} and from 0.33 to 0.92 g C m^{-2} d^{-1} for a density of 260 ind. m^{-2} (Fig. 6). The averaged annual CR was estimated to be 166 ± 149 g C m^{-2} yr^{-1} for a null density, 221 ± 157 g C m^{-2} yr^{-1} for a density of 260 ind. m^{-2}, and 528 ± 200 g C m^{-2} yr^{-1} for a density of 1700 ind. m^{-2}, representing ca. 20 g C m^{-2} yr^{-1} per 100 ind. m^{-2} (Fig. 6).

DISCUSSION

Community respiration and the effect of *Crepidula fornicata* density

Crepidula fornicata CR measured in our study at Stn HD is higher than most rates previously reported for temperate suspension feeder communities (1 to 4 mmol C m^{-2} h^{-1}; Doering et al. 1987, Gibbs et al. 2005, Migné et al. 2005), while CR measured at Stn LD is in agreement with those measured in coastal sediment

communities (0.5 to 2 mmol DO or C m^{-2} h^{-1}; Cook et al. 2004, Gibbs et al. 2005) and in the lowest range of those reported for organic matter enriched sediments impacted by shellfish cultures (1 to 4 mmol DO m^{-2} h^{-1}; Hatcher et al. 1994, Mazouni et al. 1996, Thouzeau et al. 2007).

Large differences in CR were observed between stations with high (Stn HD) and low (Stn LD) *Crepidula fornicata* densities from spring to autumn, which were 2- to 4-fold higher at Stn HD than at Stn LD. In winter, CR at Stn HD was only 1.5-fold higher than at Stn LD. Differences in CR between sites are related to *C. fornicata* biomass, as illustrated by the strong positive linear relationships between biomass and CR. The small difference in CR between Stns HD and LD in winter may be explained by a reduction in *C. fornicata* respiration rate when temperature decreases (Martin et al. 2006). *C. fornicata* respiration at Stn HD, estimated from allometric relationships (Martin et al. 2006; Table 5), accounts for
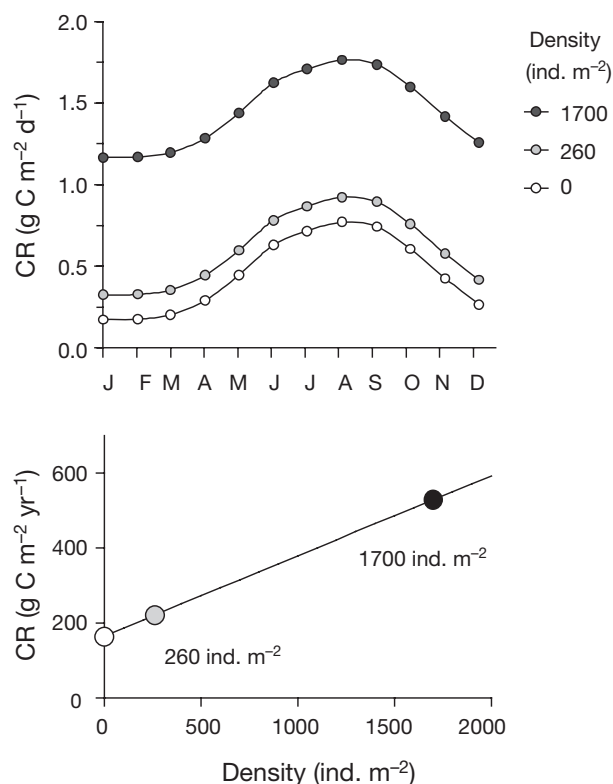

Fig. 6. Evolution of estimated daily community respiration (CR) in sites displaying densities of 0, 260, and 1700 ind. m^{-2}, and estimation of annual CR vs. *Crepidula fornicata* density

ca. 30% of CR in winter versus 40 to 60% from spring to autumn. Accordingly, sediment respiration without *C. fornicata* (*b* coefficient, Table 3) accounts for 90% of CR in winter and 30 to 40% from spring to autumn at Stn HD.

The accumulation of organic matter from *Crepidula fornicata* biodeposition also enhances oxygen consumption rates and potentially limits oxygen penetration in the sediments (Christensen et al. 2003). The resulting anaerobic environment under the sediment surface promotes ammonification and sulfate reduction (Rowe et al. 2002). Accordingly, measured community TA changes (F_{TA}) were positive, except in spring at Stn HD, indicating that processes increasing TA (ammonification, $\Delta TA = +2$ equiv. and sulfate reduction, $\Delta TA = +2$ equiv.) were predominant in the community. TA fluxes due to these processes (F'_{TA}) were up to 4-fold higher at Stn HD than at Stn LD, reflecting higher ammonification and sulfate reduction rates where biodeposition was enhanced. The increase of F'_{TA} in summer–autumn at Stn HD is also consistent with the DO depletion in the water column and the high metabolism (respiration and biodeposition) of *C. fornicata* during this period.

In this study, a comparison of CR using contrasting densities of *Crepidula fornicata* was performed at 2 different stations. Since we do not have any information on the environmental variability of CR between stations, even if they are located nearby, further investigations on spatial variability of CR are required to improve our knowledge of the effect of *C. fornicata* density on CR.

Environmental factors regulating community respiration

CR showed a distinct seasonal pattern primarily related to water temperature, as illustrated by the strong positive relationships between temperature and respiration. Such a coupling between temperature and sediment respiration rates has been well documented (Doering et al. 1987, Hatcher et al. 1994, Eyre & Ferguson 2005). The influence of organic matter sedimentation from the water column on sediment respiration is also well established (Banta et al. 1995, Rysgaard et al. 1998). Chl *a* concentration in the water column positively influenced CR_{DO}. Chl *a* concentration is an indicator of phytoplankton biomass in the water column and reflects the delivery of fresh organic matter to the sediments (Stenton-Dozey et al. 2001, Eyre & Ferguson 2005). The feeding activities of *C. fornicata* (filtration + biodeposition) are also related to phytoplankton biomass, as well as the subsequent

biodeposit remineralization (Stenton-Dozey et al. 2001). Accordingly, CR in spring is clearly enhanced by the delivery of organic matter from the phytoplanktonic bloom that occurs in May in the Bay of Brest. Despite low spring temperature (14°C), CR in this season was about 1.5-fold higher than that in autumn (15°C) and was similar to that observed in summer (17.5°C). There was also a seasonal pattern in CRQ, with CRQ <1 in winter–spring but >1 in summer–autumn. CRQ < 1 occurs when accumulated reduced equivalents are oxidized, while CRQ > 1 occurs when reduced equivalents are stored, most likely because of enhanced carbon decomposition through sulfate reduction (Eyre & Ferguson 2005). CRQ > 1 in summer-autumn is consistent with the increase of F'_{TA} in summer–autumn indicating sulfate reduction processes.

Implication of *Crepidula fornicata* invasion on carbon budget in impacted areas

The invasive species *Crepidula fornicata* affects community metabolism and thus induces changes in carbon cycling. Through respiration and feeding activities, *C. fornicata* proliferation enhances pCO_2 in seawater and may contribute to the release of CO_2 to the atmosphere. The respiration of the other components of the community, micro-, meio- and macro-organisms, also contributes to the increase of pCO_2 in seawater. CR in sites with high *C. fornicata* densities (530 g C m^{-2} yr^{-1}) falls within the highest range of values reported for communities displaying high mollusk densities (230 to 600 g C m^{-2} yr^{-1}; see review by Chauvaud et al. 2003). Carbon release from CR estimated for the mean *C. fornicata* density (260 ind. m^{-2}) is higher than carbon uptake from phytoplanktonic (148 g C m^{-2} yr^{-1}; Del Amo 1996) and microphytobenthic (20 to 40 g C m^{-2} yr^{-1}; Ni Longphuirt 2006) produc-

Table 5. *Crepidula fornicata.* Mean ± SD seasonal respiration (mmol DIC m^{-2} h^{-1}) of the population and differences with total benthic community respiration at Stn HD. Percentage of *C. fornicata* respiration in the community is also given. Respiration of the *C. fornicata* population was estimated per m^2 from seasonal size frequency distributions and densities measured at Stn HD, and from seasonal allometric relationships between *C. fornicata* shell length and body weight and between body weight and respiration rates reported by Martin et al. (2006)

Season	*C. fornicata* respiration	Difference	%
Winter	0.49 ± 0.20	0.98 ± 0.63	33
Spring	2.81 ± 1.08	1.79 ± 1.86	61
Summer	2.48 ± 0.83	3.38 ± 1.50	42
Autumn	2.90 ± 0.94	1.78 ± 2.57	62

tion in the Bay of Brest, suggesting a net increase of pCO_2 in seawater, and thus a possible efflux of CO_2 to the atmosphere. Considering the whole surface of the Bay of Brest (180 km^2), the proliferation of *C. fornicata* since the pre-invasion, 50 yr ago, to the present situation has increased carbon release by a factor of 1.5, corresponding to 10 000 tons C yr^{-1}. Considering a potential scenario of a total colonization of the bay by *C. fornicata* at ca. 1700 ind. m^{-2}, the additional carbon release in seawater since the pre-invasion may be up to 5 Gmol C yr^{-1}, corresponding to 65 000 tons C yr^{-1}. In addition, CO_2 released by calcification may enhance the given values of calculated community carbon production by 10 % if we consider that carbon release by *C. fornicata* shell calcification represents 20 % of carbon release by *C. fornicata* respiration (Martin et al. 2006), the latter corresponding to ca. 50 % of carbon release by CR. Thus, the impact of *C. fornicata* must not be considered only at population or community levels (De Montaudouin & Sauriau 1999, Chauvaud et al. 2000, Thouzeau et al. 2000), but also in terms of the carbon source, especially in a context of global change.

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