Contribution of a Dense Population of the Brittle Star *Acrocnida brachiata* (Montagu) to the Biogeochemical Fluxes of CO_2 in a Temperate Coastal Ecosystem

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Abstract The production of organic matter and calcium carbonate by a dense population of the brittle star *Acrocnida brachiata* (Echinodermata) was calculated using demographic structure, population density, and relations between the size (disk diameter) and the ash-free dry weight (AFDW) or the calcimass. During a 2-year survey in the Bay of Seine (Eastern English Channel, France), organic production varied from 29 to 50 g_{AFDW} m^{-2} $year^{-1}$ and $CaCO_3$ production from 69 to 104 g_{CaCO_3} m^{-2} $year^{-1}$. Respiration was estimated between 1.7 and 2.0 mol_{CO_2} m^{-2} $year^{-1}$. Using the molar ratio (ψ) of CO_2 released: $CaCO_3$ precipitated, this biogenic precipitation of calcium carbonate would result in an additional release between 0.5 and 0.7 mol_{CO_2} m^{-2} $year^{-1}$ that represented 23% and 26% of total CO_2 fluxes (sum of calcification and respiration). The results of the present study suggest that calcification in temperate shallow environments should be considered as a significant source of CO_2 to seawater and thus a potential source of CO_2 to the atmosphere, emphasizing the important role of the biomineralization (estimated here) and dissolution (endo-skeletons of dead individuals) in the carbon budget of temperate coastal ecosystems.

Introduction

Precipitation of biogenic calcium carbonate ($CaCO_3$) is nearly exclusively restricted to marine environments. It has been widely investigated in tropical ecosystems (Gattuso et al. 1996; Chisholm and Barnes 2005) and in the open ocean (Balch et al. 1992, 2007; Holligan et al. 1993; Garcia-Soto et al. 1995) but is still poorly documented for the temperate coastal ecosystems. Chave (1967) reviewed the definition of the carbonate sediments from a geologist's point of view and concluded that their distribution is not only restricted to shallow tropical waters where they characterize paleoenvironmental conditions. Moreover, he pointed out that (first), in temperate and cold-water shallow seas, some organisms are able to produce large amounts of calcium carbonates in the form of calcite, aragonite, or magnesium calcite at a high rate and (second) the enrichment of the sediment with calcium carbonates is mainly due to the biological activity of calcareous benthic communities. In the English Channel, the carbonate sediments are of two origins, Holocene and present (Reynaud et al. 1999). The description and the dating of the various carbonated fractions in the thanato-coenosis are the keys to understanding the mechanisms that are responsible for the accumulation of $CaCO_3$ in the sediments (Reynaud et al. 1999; Stride et al. 1999). Besides the mid- to long-term accumulation of $CaCO_3$ and hence of

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Carbon into the seafloor, biogenic precipitation is also responsible for the instantaneous consumption of carbonate alkalinity (Eq. 1). Due to thermodynamic equilibrium, this leads to the release of carbon dioxide (CO_2) in the surrounding water (Ware et al. 1991).

$$Ca^{2+} + 2HCO_3^- \longrightarrow CaCO_3 + CO_2 + H_2O \qquad (1)$$

For each mole of biogenic calcium carbonate precipitated, one mole of dissolved CO_2 is released to the medium. Due to the strong buffering capacity of the dissolved carbonate system in seawater, the amount of CO_2 released by calcification is lower than suggested by the stoichiometry of Eq. 1. The *released CO_2* to *precipitated carbonate* ratio (Ψ) is close to 0.6 under standard pCO_2 conditions and will increase with increasing pCO_2 and decreasing temperature (Frankignoulle 1994).

The English Channel, especially its western part, is considered to be abnormally rich in recent carbonate deposits, principally of biogenic origin (Reynaud et al. 1999), which suggests an intense contemporary benthic activity. Some estimates of biogenic production of calcium carbonate by benthic species or communities (Smith 1972; Beukema 1980, 1982; Potin et al. 1990; Migné et al. 1998; Chauvaud et al. 2003; Golléty et al. 2008) display values ranging between 10 and 1,800 g_{CaCO3} m^{-2} year^{-1}, i.e. up to the same magnitude as the estimates for the average calcification of an entire coral reef (Gattuso et al. 1998). However, few studies have to date investigated the air–sea CO_2 fluxes associated to biomineralization. Coral reefs and pelagic systems (e.g., due to coccolithophorid blooms) have shown an air–sea CO_2 disequilibrium (Gattuso et al. 1996; Buitenhuis et al. 1996) due to CO_2 release by calcification.

In addition, mollusk farming is particularly developed on numerous shores, particularly on French coasts (mainly *Mytilus edulis* and *Crassostrea gigas* cultivation), and it is assumed to generate both supplementary organic and $CaCO_3$ productions, then supplementary CO_2 fluxes due both to respiration and $CaCO_3$ precipitation processes.

Only few authors, to date, have investigated the potential acidification of the surrounding seawater by macrobenthic communities in temperate ecosystems (Migné et al. 1998; Chauvaud et al. 2003; Golléty et al. 2008). Given the diversity of species and biotopes concerned by these processes, it seems obvious that the role of temperate coastal benthic communities in the CO_2 fluxes appears largely underestimated. Most studies such as ecosystem carbon fluxes modeling generally do not take into account calcification processes and their consequences.

The purpose of this study is to investigate the role of a dense population in terms of biomass, calcimass (as the mass of calcium carbonate precipitated), organic and $CaCO_3$ gross productions, and CO_2 fluxes during a 2-year survey in a temperate ecosystem. The originality of our approach is to reconsider some data obtained on the brittle star *Acrocnida brachiata* population in the Bay of Seine (Gentil and Zakardjian 1990) to demonstrate the usefulness of ancient surveys in reconstructing CO_2 fluxes in the contemporary context of ocean acidification (Caldeira and Wickett 2003). Those data were only partly published to describe the reproductive cycle of the species.

Material and Methods

The Brittle Star *Acrocnida brachiata*

The common brittle star *A. brachiata* (Montagu) (Ophiuroidea: Echinodermata) is an infaunal suspension feeder found in dense aggregations on sandy bottoms of Northern Europe (Bourgoin and Guillou 1990). The arms and the dorsal and ventral surfaces of the disk are covered in calcified scales and form a calcareous endoskeleton. *A. brachiata* has a well-defined annual reproductive cycle without a sexual pause (Bourgoin and Guillou 1990; Gentil and Zakardjian 1990). The spawning period takes place in May–June and does not coincide with the annual temperature peak (Gentil and Zakardjian 1990). Reproductive studies on the species indicate an abbreviated larval development (Muths et al. 2006), allowing young individuals to settle in the spawning zone. Bourgoin et al. (1991) described the population dynamics of the species in the Douarnenez Bay and gave information about the distribution of postlarvae, the adult density, and the growth rate. Investigations realized through four surveys (1986, 1987, 1988, and 1991) revealed that *A. brachiata* always appeared as the second or third most abundant species of the *Abra alba–Pectinaria koreni* muddy-fine sand community of the Bay of Seine (Thiébaut et al. 1997). More recent surveys completed in 1996, 2001, and 2006 confirmed that *A. brachiata* remained one of the dominant species of the community (unpublished data). Unfortunately, these recent surveys were carried out once during these years and did not allow us to estimate the secondary production of the population.

Sampling Procedure

Sampling was realized at 10-m depth, using ten samples of a 0.1-m² Smith-McIntyre grab, from May 1981 to September 1983, at the station A (49° 27′ 12″ N; 0° 1′ 30″ E) in the Bay of Seine (Eastern English Channel), a macrotidal estuary (Gentil et al. 1986). Samples were sieved on a 1-mm circular mesh and retained material was preserved in 10% neutral formalin.

Individual body size was measured as the diameter of the disk on the dorsal side, from the base of one arm to the opposite interradius (Guille 1964).

Determination of Size to Biomass and Calcimass Relationships

The dry weight of brittle stars was measured after a 48 h drying at 60°C, and the ash-free dry weight (calcinations during 6 h at 520°C) was measured on 166 complete individuals by subtracting the weight of ashes (i.e., the calcimass) from the dry weight.

The relationships linking the biomass (ash-free dry weight) and the calcimass (weight of ashes) to the diameter of the disk are of the form of a power law:

$$W_{(g)} = a \times D_{(mm)}^b \tag{2}$$

The biomass (g_{AFDW}) and the calcimass (g_{CaCO3}) are given in grams (±0.01 mg). The diameter (D) of the disk is expressed in millimeter (±0.1 mm).

Demographic Structure

The demographic structure of the community was gathered from the separation of length–frequency distribution into component normal distributions, realized with the NORM-SEP method (Tomlison 1971) adapted by Gros and Cochard (1978). The program includes a method of smoothing histograms by a mobile averaging process and a discrimination of the overlapping Gaussian components using the method of Bhattacharya (1967).

Organic production calculation is based on mean body-weight increase (Crisp 1984), resulting from individual increase in the population between two samplings. For each cohort, the production can be calculated following Eq. 3.

$$Pr_t = \frac{(W_t - W_{t-1}) \times (N_t + N_{t-1})}{2} \tag{3}$$

where Pr_t is the integrated cohort production between times $t-1$ and t. W_t and N_t are the individual weight and the number of individuals at time t, respectively.

Estimation of CO_2 Fluxes

Calculations of the *released CO_2* to *precipitated carbonate* ratio Ψ were achieved according to Frankignoulle et al. (1995), considering 340 ppm of mean atmospheric CO_2 in 1981–1983. Here, we hypothesized that the basin behaved as an open system with no stratification. In situ pCO_2 values and the dissolved inorganic carbonate system characteristics were averaged after Borges and Frankignoulle (2003) to fit our temporal classes (Table 1).

Table 1 *Acrocnida brachiata*: estimations of Ψ, pCO_2, and measured temperature for each period between samplings

Period	Ψ	pCO_2 (ppm)	Temperature (°C)
May–Jun 1981	0.682	327	12.5
Jun–Jul 1981	0.664	340	15.3
Jul–Sep 1981	0.674	380	16.5
Sep–Nov 1981	0.688	381	14.8
Nov–Jan 1982	0.696	373	13.5
Jan–Mar 1982	0.720	371	10.5
Mar–May 1982	0.716	342	9.5
May–Jun 1982	0.668	327	14,0
Jun–Jul 1982	0.652	340	16.5
Jul–Aug 1982	0.642	369	19.5
Aug–Sep 1982	0.650	394	20,0
Sep–Nov 1982	0.692	381	14.5
Nov–Jan 1983	0.730	373	9.5
Jan–Mar 1983	0.744	371	8.0
Mar–May 1983	0.720	342	9.0

The annual flux of CO_2 associated with respiration has been estimated by analogy in density, size–weight relationship, and respiration rate estimated for the brittle star *Ophiothrix fragilis* (0.00192 g_C g_{AFDW}^{-1} day^{-1}, Migné and Davoult 1997), as several authors showed that different temperate ophiuroid species, even living in different sedimentary environments, presented very close metabolic rates when expressed per gram of dry weight (Farmanfarmaian 1966; Migné and Davoult 1997 and references herein).

Results

Demographic Structure and Productions

The relationships linking the biomass (ash-free dry weight) and the calcimass (weight of ashes) to the diameter of the disk were:

$$\text{Biomass}(g_{AFDW}) = 0.00001 \times D^{3.981}, \; n = 166, \; R^2 = 0.940 \tag{4}$$

$$\text{Calcimass}(gCaCO_3) = 0.00047 \times D^{2.713}, \; n = 166, \; R^2 = 0.953 \tag{5}$$

The second one is illustrated in Fig. 1.

The mean density (±standard deviation) of the population of *A. brachiata* reached 910 (±315) ind m^{-2}. Extreme values were found in May and September 1981, respectively, 370 and 1,576 ind m^{-2} (Gentil et al. 1986). The
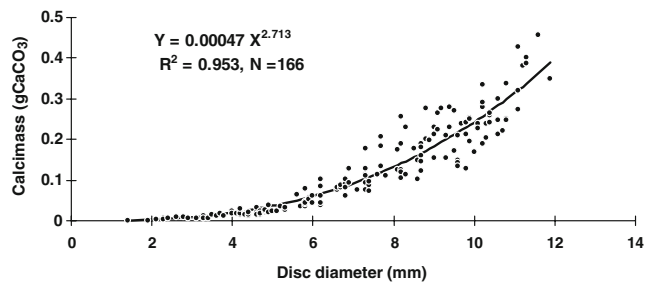
Fig. 1 Size: weight allometric relationship between Calcimass (g) and disk diameter (mm) in *Acrocnida brachiata*

histograms of size frequency indicated that the density of the population globally increased through summer and autumn when the recruitment occurred and displayed a plateau in winter. The population showed a polymodal size structure (Fig. 2), characteristic of the co-occurrence of different cohorts within the same population. The growth curves of the different cohorts (Fig. 3) were obtained from the histograms of size frequency. Recruitments appeared in July 1981, June 1982, and September 1983 and produced a new cohort. A maximum of five cohorts (1978–1982) was found in June 1982, cohort 1978 disappeared while cohort 1982 was recruited. This indicated that the mean longevity of the species could be 4 or 5 years.

The biomass and calcimass of the population were calculated from the dynamics of the species and the size–weight relationships. The average biomass was, respectively, 31.0 ($\pm$12.11) and 28.3 ($\pm$8.20) g_{AFDW} m^{-2} and the average calcimass was, respectively, 85.1 ($\pm$32.12) and 85.5 ($\pm$22.04) g_{CaCO3} m^{-2} for the first and the second year of study.

The annual organic matter production was estimated to 49.8 and 29.0 g_{AFDW} m^{-2} $year^{-1}$ for the years 1981 and 1982, respectively. The annual $CaCO_3$ production was 104.2 and 68.5 g_{CaCO3} m^{-2} $year^{-1}$, for year 1 and year 2, respectively.

The annual organic productivity (defined as the ratio between annual organic production and mean biomass) was 1.61 and 1.02 $year^{-1}$ for the 2 years of survey, whereas annual $CaCO_3$ productivity (defined as the ratio between the annual $CaCO_3$ production and the mean calcimass) was 1.22 and 0.80 $year^{-1}$, respectively.

CO_2 Fluxes Associated to the Precipitation of Calcium Carbonate and to the Respiration

The annual molar CO_2 released in the surrounding seawater was computed from the estimated $CaCO_3$ productions for each period between the different samplings and from the data of Table 1. The calcification by *A. brachiata* yielded a CO_2 flux to the atmosphere of 0.7 and 0.5 mol_{CO2} m^{-2} $year^{-1}$ during the first and the second year

of the survey, corresponding to 8.6 and 6.0 g_C m^{-2} $year^{-1}$. The respired CO_2 produced by the population was estimated, on the annual basis, to 2.0 and 1.7 mol_{CO2} m^{-2} $year^{-1}$, respectively, during the 2 years of survey. When converted into carbon units, the flux of CO_2 associated to respiration accounted for 24 and 20 g_C m^{-2} $year^{-1}$. Based on these two calculations, the computation of the relative amount of CO_2 released during $CaCO_3$ precipitation represented between 23% and 26% of the total CO_2 released by *A. brachiata*.

Discussion

The variations of density strongly followed the recruitment events, which is a general feature in numerous macrobenthic species. In the case of *A. brachiata*, the density increased in late summer and autumn. Despite these fluctuations, *A. brachiata* remained one of the dominant species of the benthic community in the Bay of Seine, in terms of surface-averaged and time-averaged density and biomass (Thiébaut et al. 1997). It is more than twice the density found in Douarnenez Bay by Bourgoin et al. (1991). Maximum growth rates appeared in spring and summer as already shown by Bourgoin et al. (1991).

Annual organic production was quite important and variable from 1 year to another, which is not surprising for a species dominating a community. Similar annual organic production levels, whether in intertidal or subtidal conditions, are often observed in other dominant species of sandy communities. Indeed, annual organic productivity is of the same order of magnitude as some values estimated for macrofauna (e.g., Rouhi et al. 2008), ranging between 0.5 and 3 $year^{-1}$ (Raffaelli and Hawkins 1999). For example, annual organic productivity of 1.28 $year^{-1}$, estimated for another coastal ophiuroid, *O. fragilis* (Davoult 1989), was very close to our observations.

The amount of CO_2 released during $CaCO_3$ precipitation is far from being negligible and represents, depending on the species, between 16% for the gastropod *Crepidula fornicata* (Martin et al. 2006) and 47% for the barnacle *Chthamalus montagui* (Golléty et al. 2008) of the total CO_2 fluxes due to both respiration and calcification. The relative amount of CO_2 released during $CaCO_3$ precipitation by *A. brachiata* represented between 23% and 26% of the total CO_2 produced. Such values are very close to the one estimated for the ophiuroid *O. fragilis* (30%, Migné et al. 1998).

The annual gross production of $CaCO_3$ was lower than some previous estimates for other calcifying coastal temperate benthic species (Migné et al. 1998; Chauvaud et al. 2003; Martin et al. 2006). It could have been slightly underestimated as our study did not take into account the possible regeneration of arms that is a common feature in
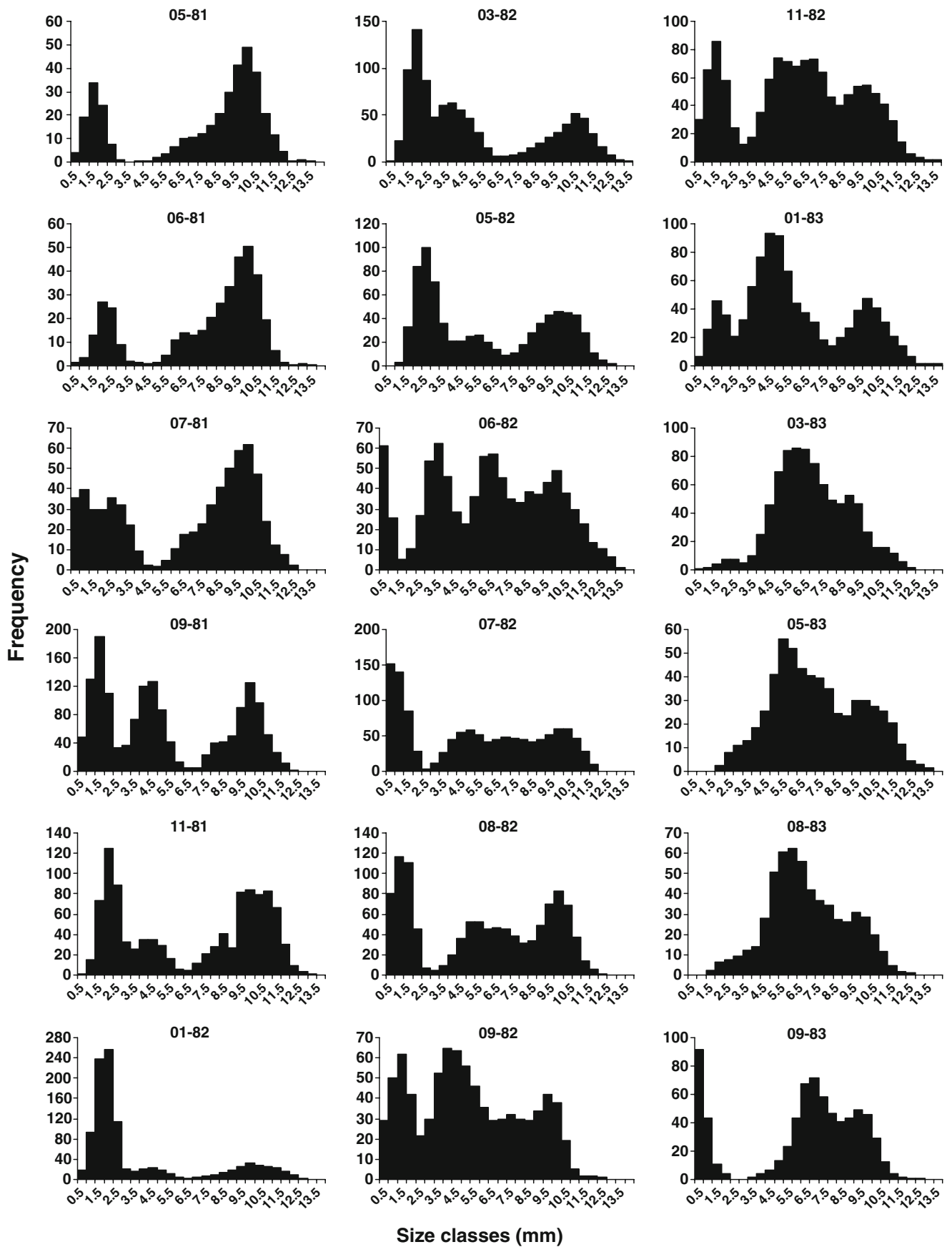
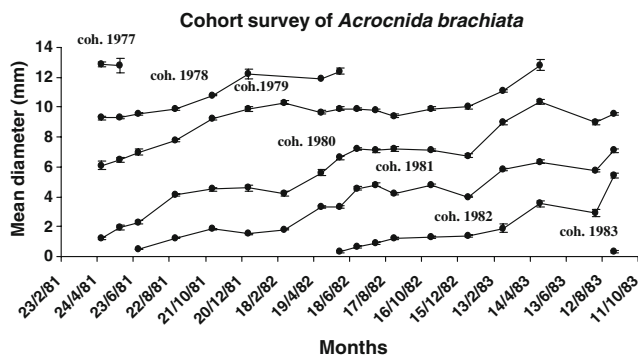Fig. 2 Size (mm)–frequency histograms from May 1981 to September 1983 of the *A. brachiata* population

Fig. 3 Cohort growth calculated from histograms of the *A. brachiata* population from May 1981 to September 1983. Values corresponded to the mean diameter (±standard deviation)

ophiuroids. However, some other abundant species within the same community are also calcifying species, such as the bivalves *Phaxas* (*Cultellus*) *pellucidus*, *Abra alba*, or the echinodermata *Echinocardium cordatum* (Thiébaut et al. 1997) and calcified algae. The assemblage of such species could potentially scale the production of $CaCO_3$ to a higher level, in the range of the one determined previously (Migné et al. 1998; Chauvaud et al. 2003; Martin et al. 2006). Recent studies, including this one, clearly showed that numerous temperate benthic communities, if not all, seem to produce very high amounts of $CaCO_3$: subtidal sandy communities (Chauvaud et al. 2003; this study), subtidal pebble communities (Migné et al. 1998), intertidal sandy/muddy communities (Beukema 1980, 1982) or intertidal rocky ones (Gollety et al. 2008), or invasive species such as the slipper limpet *C. fornicata* (Martin et al. 2006).

In the growing concern of ocean acidification (The Royal Society 2005), some recent papers pointed out the potential negative impact of lower pH and a lower saturation state with respect to calcite and aragonite on the open-ocean calcifiers, such as the coccolithophores (Riebesell et al. 2000) and pteropods (Orr et al. 2005) and some well-recognized benthic ones, like corals (Bamber 1990; Gattuso et al. 1999). However, recent studies reported scarce cases of increased calcification due to high CO_2 partial pressures, for example in the brittle star *Amphiura filiformis* (Wood et al. 2008), highlighting the complexity of the metabolic responses of organisms. The latter study however pointed out that this upregulation of calcification comes at a dramatic cost that is muscle wastage and is unlikely to be sustainable in the long term. As suggested by Shirayama and Thornton (2005) and Gazeau et al. (2007), negative effects are expected in temperate shallow benthic ecosystems where calcifying species are dominant. Such a change is able to deeply impact the carbon budget of coastal shallow areas, where more than 40% of the global $CaCO_3$ is produced (Milliman 1993) and affect the autotrophic/heterotrophic status of the

coastal zone at a global scale (Gattuso et al. 1998). Temperate marginal seas now act as sinks for atmospheric CO_2, but that sink could be almost compensated locally by CO_2 fluxes from near-shore ecosystems such as estuaries and salt marsh waters (Borges et al. 2005). For example, Borges and Frankignoulle (2003) calculated that the net CO_2 flux in the English Channel is close to zero. Among the several processes, besides net ecosystem production, that could modulate the net CO_2 flux (Borges et al. 2006), Borges and Frankignoulle (2003) pointed out that intense benthic calcification, particularly dense brittle star populations (e.g., *O. fragilis*, see Migné et al. 1998) could have a significant impact on CO_2 air–sea exchange, as in tropical coral reefs (e.g., Gattuso et al. 1993).

Conclusion

Our study demonstrates that calcification process, which is a common process in shallow temperate seas, appears as a nonnegligible source of CO_2 in coastal ecosystems, even if a part of the $CaCO_3$ produced will be dissolved at a short timescale. Cugier et al. (2005) estimated gross phytoplanktonic primary production around 250–300 g_C m^{-2} $year^{-1}$ in the part of the Bay of Seine where this population takes place: CO_2 production both by gross calcification and respiration of the *A. brachiata* population (i.e., only one species among several calcifying ones) could then represent up to 10% of the CO_2 fixed by pelagic primary production. The example of the brittle star *A. brachiata* illustrates that numerous estimations could be easily calculated from population dynamics already realized on several calcified abundant species, natural as well as cultivated, that could contribute to reduce the relative uncertainty on CO_2 flux of several near-shore ecosystems (Borges 2005).

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