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NOTE

Calcium carbonate production of a dense population of the brittle star *Ophiothrix fragilis* (Echinodermata: Ophiuroidea): role in the carbon cycle of a temperate coastal ecosystem

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ABSTRACT: The production of calcium carbonate by a dense *Ophiothrix fragilis* population was calculated in order to investigate its role in the carbon budget of a temperate coastal ecosystem (Dover Strait, eastern English Channel). Production, calculated using monthly data of population density, demographic structure and a size/$CaCO_3$ conversion, was 682 g $CaCO_3$ m^{-2} yr^{-1} Assuming that the molar ratio of CO_2 released to $CaCO_3$ precipitated varied with temperature between 0.66 and 0.73, this production would result in the release of 4.8 mol CO_2 m^{-2} yr^{-1}. This calculation reinforces the suggestion that this coastal system is a source of CO_2 to the atmosphere.

KEY WORDS: CO_2 flux · $CaCO_3$ production · Ophiuroid · Coastal ecosystem · Temperate sea

The precipitation of calcium carbonate decreases the concentration of dissolved inorganic carbon (DIC) in seawater by 1 mole for each mole of $CaCO_3$ precipitated (dissolution of $CaCO_3$ has the opposite effect):

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$$

Calcification also induces a shift in the seawater carbonate system that generates dissolved CO_2. Precipitation of $CaCO_3$ is therefore a source of CO_2 in seawater (Ware et al. 1992). The molar ratio (Ψ) of CO_2 released versus $CaCO_3$ precipitated is 0.6 at 25°C for present 'standard' seawater (pCO_2 = 356 µatm; total alkalinity = 2370 µEq kg^{-1}; S = 35) (Frankignoulle et al. 1994)

The contribution of $CaCO_3$ precipitation in the carbon cycling of tropical marine ecosystems, mostly coral reefs, has been extensively investigated during the last 10 yr (reviewed by Gattuso et al. 1998). Most coral reefs investigated so far have been shown to be sources of CO_2 to the atmosphere because, on a 24 h basis, CO_2 release by community calcification is higher than the uptake of CO_2 resulting from net community production. Blooms of coccolithophorids, possibly the most important calcifying marine organisms (Westbroek et al. 1989), have also received a lot of attention and have been shown to be net sources of CO_2 to the atmosphere (Robertson et al. 1994). The precipitation of $CaCO_3$ has received comparatively much less attention in coastal temperate ecosystems, despite the fact that some of them harbour dense populations of calcifying organisms such as calcareous algae, bryozoans, molluscs or polychaetes (e.g. Smith 1972, Collins 1986). The purpose of this paper is to investigate the role (in terms of CO_2 fluxes) of the production of $CaCO_3$ of a dense ophiuroid *Ophiothrix fragilis* (Abildgaard) population in such a coastal area (Dover Strait, eastern English Channel).

Ophiothrix fragilis is widely distributed in the eastern Atlantic, from northern Norway to the cape of Good Hope (Moyse & Tyler 1990). It forms dense beds on all coasts of the English Channel, mainly on coarse sediments subject to high tidal currents (Vevers 1952, Cabioch 1968, Cabioch & Glaçon 1975, 1977), and also on muddy gravels bottoms (Warner 1971). These dense aggregations of this passive suspension-feeder, feeding mainly on phytoplankton (Warner & Woodley 1975), are assumed to have a significant effect on the exchanges of organic matter at the water-sediment interface (Hily 1991, Davoult et al. 1998). In the Dover Strait, a well-mixed coastal area (Pingree et al. 1975) where tidal currents exceed 2 m s^{-1} in spring tide (Anonymous 1988), the pebble epifaunal community is dominated by this organism at high densities (up to

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2000 ind. m^{-2}; Davoult 1990). The areal extent of the *O. fragilis* population is approximately 600 km^2 in the Dover Strait and 5400 km^2 in the eastern English Channel (Sanvicente Anorve 1995). $CaCO_3$ production can be calculated using the density of the population, its demographic structure and the relationship of size versus $CaCO_3$ content. The data sets are shown in Table 1. Density data were obtained on samples collected by scuba divers in the Dover Strait from June 1992 to June 1993 (Migné & Davoult 1997). The station was located in the coastal part of the population (50° 55' 5 N; 1° 34' 7 E) at a depth of 37 m. Salinity varied from 34.6 to 34.9 (Migné 1996). Size distribution and cohort surveys were made on individuals collected in the same station from February 1987 to March 1988 (Davoult et al. 1990). The size versus $CaCO_3$ content relationship was established for the species by Davoult et al. (1992).

Production of $CaCO_3$ by the Dover Strait *Ophiothrix fragilis* population (i.e. the sum of production between each sampling period, see Table 1) is estimated to be 682 g m^{-2} yr^{-1}. This value is higher than any estimates of carbonate production found in the literature for subtidal macrobenthic communities or populations in temperate ecosystems. Smith (1972) gave subtidal rates of $CaCO_3$ production by calcareous organisms near 400 g m^{-2} yr^{-1} at 3 localities along the southern California coastline. The major producers of $CaCO_3$ in that hard-bottom environment were bryozoans and coralline algae and, to a lesser extent, echinoderms and molluscs. Medernach (1996) calculated the carbonate production of a polychaete population at different stations (with different densities of the species) in the Bay of Banyuls (Mediterranean Sea, France). She found values varying from 0.7 g $CaCO_3$ m^{-2} yr^{-1} (for a station with 35 ind. m^{-2}) to 397 g m^{-2} yr^{-1} (for a station with 3550 ind. m^{-2}). Collins (1986) estimated a carbonate production of 330 g m^{-2} yr^{-1} for a deep water *Modiolus*-brachiopod assemblage from the west coast of Scotland. In this assemblage, *O. fragilis* accounted for 7.4 % of the total biomass (expressed as ash free dry weight) and for 20.9% of the total $CaCO_3$ production. In that study, $CaCO_3$ production was calculated using an estimate of the production of the population (in terms of ash free dry weight) and a 'standard conversion figure' of 3.46 (our data gave a conversion figure of 2.69). The calculated $CaCO_3$ production rate of the species is on the same order of magnitude in the 2 studies: 445 mg $CaCO_3$ ind.$^{-1}$ yr^{-1} according to Collins' data and 541 mg $CaCO_3$ ind.$^{-1}$ yr^{-1} according to our data. Our estimate of the daily calcification rate is 1.9 g $CaCO_3$ m^{-2} d^{-1}, a figure that is not negligible compared with the calcification rates reported in the literature for the major calcifying systems. The calcification rates of dense coral communities can be as high as 34 g $CaCO_3$ m^{-2} d^{-1}, but the average calcification rate of entire reef systems is much lower, ca 3 g $CaCO_3$ m^{-2} d^{-1} (Gattuso et al. 1998). A rate of calcification of 1.7 g $CaCO_3$ m^{-2} d^{-1} was observed during the survey of a coccolithophorid bloom in the North East Atlantic (Holligan et al. 1993). Our results confirm that significant $CaCO_3$ deposition can occur in coastal temperate ecosystems, as previously emphasized by Smith (1972). Other temperate systems, such as non exploited formations of maerl (Pinot 1997) or exploitation of oysters or mussels, are also likely sites of elevated rates of calcification.

The ratio of CO_2 released to $CaCO_3$ precipitated depends on temperature (Frankignoulle et al. 1994), it varies between 0.66 and 0.73 in the Strait of Dover (Table 2). Calcium carbonate production estimated in the *Ophiothrix fragilis* population (6.8 mol $CaCO_3$ m^{-2} yr^{-1}) would thus result in the release of 4.8 mol CO_2 m^{-2} yr^{-1} (i.e. 58 g C m^{-2} yr^{-1}). The role of the *O. fragilis* population in the Dover Strait has already been studied by constructing a model of fluxes and production of organic carbon (Davoult et al. 1998). According to this model, the input of organic carbon into the '*O. fragilis*

Table 1. Mean diameter (*D*), mean $CaCO_3$ content and density of each cohort for each sampling period in the Dover Strait *Ophiothrix fragilis* population. The average $CaCO_3$ content was calculated according to the following relationship: $\log(CaCO_3) = 0.258 + 2.53\log D$ (Davouilt et al. 1992)

Period	Mean diameter (mm)	Mean $CaCO_3$ content (mg ind.$^{-1}$)	Density (ind. m^{-2})
February	7.4	286.4	1169
	1.9	9.2	81
April	9.3	510.5	747
	3.9	56.6	91
	1.2	2.9	31
May	10.3	660.7	1006
	4.9	100.9	68
	1.9	9.2	68
June	10.9	763.8	1117
	7.1	258.0	127
	4.1	64.3	92
	1.2	2.9	78
August	10.8	745.7	943
	7.6	306.5	225
	4.2	68.4	329
September	9.8	583.2	662
	7.7	316.8	190
	3.2	34.4	458
October	9.7	568.2	662
	4.1	64.3	415
November	9.7	568.2	900
	5.0	106.3	386
December	9.2	497.0	892
	6.1	175.7	382
February	8.9	457.0	1188
	0.7	0.7	62

Table 2. Mean bottom temperature (T) in the Dover Strait and molar ratio of CO_2 released versus $CaCO_3$ precipitated (ψ) at each period used for the calculation of $CaCO_3$ production of the *Ophiothrix fragilis* population. ψ is calculated according to the following relationship: $\psi = 0.8 - 8.3 \times 10^{-3}T$ (Frankignoulle et al. 1994)

Period	Mean bottom temperature (°C)	ψ
Feb to Apr	8.1	0.73
Apr to May	10.8	0.71
May to Jun	13.3	0.69
Jun to Aug	15.9	0.67
Aug to Sep	16.7	0.66
Sep to Oct	15.4	0.67
Oct to Nov	13.3	0.69
Nov to Dec	10.8	0.71
Dec to Feb	8.1	0.73

compartment' exceeds local primary production. Input was 635 g C m^{-2} yr^{-1} (calculated both as the annual fluxes of ingestion and as the sum of annual fluxes of respiration, egestion and production) and phytoplankton primary production was 336 g C m^{-2} yr^{-1} according to Quisthoudt (1987) or 227 g C m^{-2} yr^{-1} according to Hoch (1995). Phytoplankton is assumed to be the only primary producer in this area where light limitation (37 m deep with a high concentration of suspended material) does not allow the development of phytobenthos. It was concluded that this temperate coastal ecosystem is net heterotrophic, since community consumption is apparently larger than gross primary production and the system is thus a potential source of CO_2 to the atmosphere. This conclusion, based on the organic carbon budget, is strengthened by the results of the present paper which demonstrate that the calcium carbonate deposition is a significant additional source of CO_2 to seawater.

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