Clams as CO_2 generators: The *Potamocorbula amurensis* example in San Francisco Bay

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Abstract

Respiration and calcium carbonate production by the invasive Asian clam, *Potamocorbula amurensis,* were calculated to assess their importance as CO_2 sources in northern San Francisco Bay. Production, calculated using monthly population density and size structure measured at three sites over 7 yr and a shell length/$CaCO_3$ conversion factor, averaged 221 ($\pm$184) g $CaCO_3$ m^{-2} yr^{-1}. Net calcium carbonate production by this exotic bivalve releases CO_2 at a mean rate of 18 ($\pm$17) g C m^{-2} yr^{-1}. Respiration by *P. amurensis,* estimated from secondary production, releases additional CO_2 at a mean rate of 37 ($\pm$34) g C m^{-2} yr^{-1}. Therefore, total net CO_2 production by *P. amurensis* averages 55 ($\pm$51) g C m^{-2} yr^{-1} in an estuarine domain where net primary production consumes only 20 g inorganic C m^{-2} yr^{-1}. CO_2 production by *P. amurensis* in northern San Francisco Bay is an underestimate of the total CO_2 supply from the calcified zoobenthic communities of San Francisco Bay, and results from other studies have suggested that this rate is not unusual for temperate estuaries. Global extrapolation yields a gross CO_2 production rate in the world's estuaries of 1×10^{14} g C yr^{-1}, which suggests that calcified benthic organisms in estuaries generate CO_2 equal in magnitude to the CO_2 emissions from the world's lakes or from planetary volcanism (the net source is determined by the highly variable rate of CO_2 consumption by carbonate dissolution). This biogenic CO_2 source is increasing because of the continuing global translocation of mollusks and their successful colonization of new habitats.

The combination of a unique level of global warming in the late 20th century and narrowed constraints on the role of natural variability provide growing evidence that a greenhouse effect from anthropogenic CO_2 emissions can be distinguished from natural variability in the climate system (Crowley 2000). However, there remain large uncertainties in the contemporary global carbon budget and even gaps in our knowledge of the processes contributing to planetary carbon cycling (Schlesinger 1997). We have not yet identified or measured all of the important sources and sinks of CO_2, the greenhouse gas that contributes at least 50% to projected global warming (Lashof and Ahuja 1990). Carbon dioxide uptake by photosynthesis and its release by respiration are major processes by which marine organisms alter the concentration of carbon dioxide in seawater. Another set of biologically mediated reactions, precipitation and dissolution of calcium carbonate, may also contribute to the global CO_2 balance (Gattuso 1996). Calcification induces shifts in the seawater carbonate equilibrium to generate dissolved CO_2 and is therefore a source of CO_2 (Wollast et al. 1980). The deposition of one mole of calcium carbonate (Ca^{2+} + $2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$) releases nearly one mole of CO_2 in freshwater and ~0.6 moles of CO_2 in seawater (Ware et al. 1992). Photosynthesis, respiration, calcification, and calcite dissolution are tightly coupled in marine systems.

The increase in $p$$CO_2$ from biogenic calcification has been well documented (Berger 1982), especially for tropical coral reefs, which are net sources of CO_2 to the atmosphere (Gattuso et al. 1998). However, the impact of biogenic $CaCO_3$ precipitation on CO_2 production in temperate coastal ecosystems has received much less attention (Wollast 1994). Migné et al. (1998) assessed the importance of calcification by dense populations of the brittle star *Ophiothrix fragilis* in the English Channel and showed that this biogenic source of CO_2 can also be important in temperate coastal waters. Our interest in this process is motivated by studies in recent decades that have shown large-scale effects of invasive mollusk species in lake, river, and estuarine ecosystems (Alpine and Cloern 1992; Strayer et al. 1999). Although mollusks such as *Dreissena polymorpha, Ruditapes philippinarum, Crepidula fornicata, Potamocorbula amurensis* and *Corbicula fluminea* are among the most common invasive aquatic

Fig. 1. Study sites in northern San Francisco Bay.

Table 1. Relationships between the size (S_l, shell length in mm) of *P. amurensis* and $CaCO_3$ content of the shell (S_w) at three locations in northern San Francisco Bay (Fig. 1).

Sta.	Regression equation	n	r^2	P
4	$\ln S_w = 3.18 \ln S_l - 10.04$	75	0.976	<0.001
6	$\ln S_w = 3.26 \ln S_l - 10.17$	40	0.976	<0.001
8	$\ln S_w = 3.19 \ln S_l - 10.06$	135	0.988	<0.001

organisms, CO_2 released by their shell synthesis has never been assessed. The purpose of the present study was to (1) estimate $CaCO_3$ and CO_2 production rates by the exotic Asian clam *P. amurensis* in San Francisco Bay, (2) review results of other studies where information is available to estimate the role of benthic mollusk production on the inorganic C budget, and (3) consider the growing effects of invasive mollusks in lakes, rivers, and estuaries on global CO_2 production.

The Asian clam in San Francisco Bay

P. amurensis (a bivalve mollusk) was introduced to San Francisco Bay in 1986 (Carlton et al. 1990), and it proliferated within 2 yr to make up to 95% of benthic biomass of colonized sediments (Nichols et al. 1990). Before this introduction, bivalves were present in the landward reaches of the estuary only during infrequent years of drought (Nichols et al. 1990). Now, *P. amurensis* is present in all water depths in a range of bottom types, along the full salinity range (<1–33; Carlton et al. 1990) throughout all seasons and years. The dense population of this suspension feeder has significantly altered the ecosystem functioning of Suisun Bay (Fig. 1) by (1) controlling the phytoplankton biomass and reducing primary production fivefold (Alpine and Cloern 1992), (2) reducing zooplankton abundance through predation and food competition, and (3) changing the benthic community structure (Nichols et al. 1990). The benthic community of Suisun Bay included few mollusks but high abundances of polychaetes and small crustaceans before 1986. Today, *P.*

amurensis dominates the macrobenthos biomass in northern San Francisco Bay.

P. amurensis as a CO_2 source to San Francisco Bay

We estimated the $CaCO_3$ production rate of *P. amurensis* collected monthly between June 1988 and November 1994 at three locations (Fig. 1), using population densities, size frequency distributions, and relationships between shell length and $CaCO_3$ content. The latter were obtained by measurements of both shell size and weight to fit empirical shell length : calcimass relationships for each station (Table 1). The density of *P. amurensis* varied between 2 and 16,000 individuals m⁻², and biomass (ash-free dry weight [AFDW]) ranged 0.6–131 g m⁻². Annual $CaCO_3$ production by the *P. amurensis* population (the sum of monthly production estimates) varied between 7 and 1,100 and averaged 221 (±184) g $CaCO_3$ m⁻² yr⁻¹ for all sites and years (Table 2). The maximum rate of 1,100 g m⁻² yr⁻¹ is one of the highest estimates of carbonate production reported in the literature for subtidal macrobenthic communities or populations in temperate ecosystems, but the mean value lies within the range commonly measured (Table 3). The estimated daily calcification rates (0.02–3 g $CaCO_3$ m⁻² d⁻¹) by this one bivalve approach rates measured in the important marine calcifying systems: coral reefs (3 g $CaCO_3$ m⁻² d⁻¹; Gattuso et al. 1998) and coccolithophorid blooms in the Northeast Atlantic (1.7 g $CaCO_3$ m⁻² d⁻¹; Holligan et al. 1993). Our results, along with those of others (Smith 1972; Migné et al. 1998; Medernach et al. 2000), illustrate the significance of biogenic $CaCO_3$ production in temperate estuaries.

We estimated the ratio of CO_2 released to $CaCO_3$ precipitated (Ψ) as a function of the mean near-bottom salinity (S) and temperature (T) measured between benthic sampling dates with moored sensors (http://iep.water.ca.gov/data.html), using the equations of Frankignoulle et al. (1994; p. 460) to define the temperature dependence of Ψ (for $S = 35$) and the inverse relationship between Ψ and salinity (at $T = 15°C$). This procedure, based on computations for $pCO_2 = 350$ μatm, yields an underestimate of Ψ in northern San Francisco Bay, where pCO_2 is >350 μatm (see below). At the pCO_2 in Suisun Bay, Ψ would increase by ~15% (Frankignoulle et al. 1994). Our estimates of Ψ in Suisun Bay fluctuated with monthly changes in bottom salinity and temperature between 0.72 and 0.97. Calcium carbonate production by *P. amurensis* would thus release 0.08–9.1 mol CO_2 m⁻² yr⁻¹, corresponding to a mean CO_2 source of 20 (±19) g C m⁻² yr⁻¹.

Some of the CO_2 released by $CaCO_3$ precipitation is ultimately removed by the reverse reaction of shell dissolution

Table 2. Estimated annual rates of $CaCO_3$ production (g m^{-2} yr^{-1}), gross CO_2 generation (g C m^{-2} yr^{-1}) from $CaCO_3$ production, and respiration of *P. amurensis,* sampled monthly at three locations in Suisun Bay.

Station	1988	1989	1990	1991	1992	1993	1994	Average	SD
8									
$CaCO_3$ production	470	560	270	180	320	1,100	130	433	331
CO_2 from $CaCO_3$ production	44	55	26	16	29	109	11	41	33
CO_2 from respiration	75	55	57	53	68	223	9	77	68
Total CO_2 released	119	110	83	69	97	332	20	119	99
4									
$CaCO_3$ production	110	320	150	47	200	7	73	130	106
CO_2 from $CaCO_3$ production	6	7	6	9	8	10	9	8	2
CO_2 from respiration	16	72	20	2	23	2	14	21	24
Total CO_2 released	22	79	26	11	31	12	23	29	23
6									
$CaCO_3$ production	72	240	190	46	120	27	15	101	86
CO_2 from $CaCO_3$ production	7	24	19	5	9	3	1	10	9
CO_2 from respiration	12	29	25	6	19	5	3	14	10
Total CO_2 released	19	53	44	11	28	8	4	24	19
All Sta., all years									
$CaCO_3$ production								221	184
CO_2 from $CaCO_3$ production								20	19
CO_2 from respiration								37	34
Total CO_2 released								57	53

Table 3. Comparison of annual $CaCO_3$ production (g m^{-2} yr^{-1}) by benthic organisms in several temperate and tropical aquatic ecosystems.

Organisms	g $CaCO_3$ m^{-2} yr^{-1}	Location	Authors
Temperate marine systems			
Bryozoans, coralline algae, echinoderms, and mollusks	400 (mean, 3 sites)	Southern California coastline, US	Smith (1972)
Polychaetes: *Ditrupa*	17–11,836	Mediterranean Sea, France	Medernach et al. (2000)
Modiolus: brachiopod assemblage	330	West coast of Scotland	Collins (1986, unpubl. data)
O. fragilis	682	Eastern English Channel, France	Migné et al. (1998)
P. amurensis	7–1,100 = 221	San Francisco Bay, US	Present study
Four sandy beach assemblages	204, 19, 25, 234 = 130	West coast of Brittany, France	Hénaff (1997, unpubl. data)
Ficopomatus reefs	650–1,200	Po River Delta, Italy	Bianchi and Morri (1996)
Tropical marine systems			
Deep-water coralline algae assemblage	190–300	Penguin Bank, Hawaii	Agegian et al. (1988)
Mollusks	7–64	Florida Bay, US	Bosence (1989)
Mollusks	3.74–309	Biscayne Bay, US	Moore (1972)
Foraminifera	2,000	Indo-Pacific reef flats	Hallock (1981)
Complete reef systems	1,008	Average net calcification ($N = 7$)	See Gattuso et al. (1998)
Benthic communities	500	Banks and embayments (tropical and subtropical environments)	See Milliman (1993)
Halimeda "meadow"	1,200–3,200	Great Bahamas Bank	Freile et al. (1995)
Seagrass epiphytes	50–526	Shark Bay, Australia	Walker and Woelkerling (1988)
Freshwater			
D. polymorpha	0–48	Great Lakes, US	Chase and Bailey (1999)
D. polymorpha	500–2,000	St. Lawrence River, US	Ricciardi et al. (1996)
C. fluminea	200–1,200	Ohio River, US	Miller and Payne (1994)
C. fluminea	200	Delta Mendota Aqueduct, California, US	Eng (1977)

(Wollast 1994), so the net CO$_2$ production is determined by the balance between carbonate precipitation and dissolution. Quantifying dissolution (Ca^{2+} fluxes) in fine-grained sediments is difficult but can be assessed with either direct measurements or estimates from diffusive-transport/reaction models. The results of such studies are often inconsistent, because CaCO$_3$ dissolution is controlled by time-dependent relationships among physical, chemical, and biological processes (Reaves 1986; Callender et al. 2002). For example, carbonate particle size (Powell et al. 1986) and burial (Powell and Davies 1990) control carbonate abrasion, fragmentation, and dissolution. Therefore, we cannot apply the results from foraminifera-derived carbonates to assess dissolution rates of large infaunal bivalves. Working on infaunal (*Mercenaria mercenaria*) and epifaunal (*Crassostrea virginica*) mollusks in intertidal mud flats and tidal creek sediments, Reaves (1986) showed strong geographical variations in calcium carbonate preservation (from no evidence to extensive dissolution after 5–15 yr) in relation to organic matter inputs at the sediment/water interface. Large inputs of organic matter stimulate sulfate reduction, leading to the supersaturation of calcium carbonate in pore waters. Rude and Aller (1991) calculated for several macrobenthic taxa (including mollusks) that only 10%–23% of the influx of calcium carbonate is dissolved during early diagenenesis (~20 yr timescale) on a mudbank of Florida Bay. Recent experimental studies demonstrated that mollusk bivalve shells held in shallow water (15 m depth) showed only minor changes in shell condition after 1 yr (Callender et al. 2002). On the basis of these results, and the facts that *Potamocorbula* is (1) an infaunal species that produces a large quantity of calcium carbonate, (2) a macrobenthic species with a large shell (>5 mm) covered by protective conchiolin layers (Kardon 1998), and (3) spreading in sediments where sulfate reduction rates are expected to be high (~17 mmol m^{-2} d^{-1} in nearby Tomales Bay; Smith and Hollibaugh 1997), we assume here an annual dissolution rate of 10%, in agreement with Milliman's (1993) estimate for semienclosed basins. Thus, the estimated mean net calcification rate in northern San Francisco Bay is 199 g CaCO$_3$ m^{-2} yr^{-1} (±165), which corresponds to a mean net CO$_2$ source of 18 (±17) g C m^{-2} yr^{-1}.

We also estimated the CO$_2$ released from *P. amurensis* respiration, using the relation $\log_{10}R = 0.367 + 0.99 \log_{10}P$ (Schwinghamer et al. 1986), where R and P are annual respiration and production, respectively (in kcal m^{-2} yr^{-1}, with 1 g C = 11.4 kcal). We calculated the secondary production of *P. amurensis* using the standard method when age classes are separable and recruitment is included (Crisp 1971). Age classes were separated using MIX, a computer program for fitting overlapping size frequency distributions (McDonald and Green 1988). Dry tissue weight was calculated for a range of animal sizes using the AFDW method (segregated sizes of animals were dried at 60°C and ashed at 500°C, with tissue weight computed as the difference between the two weights). Depending on the site (Table 2), the mean annual rate of CO$_2$ release by *P. amurensis* respiration ranged 14–77 g C m^{-2} yr^{-1}.

The mean level of CO$_2$ production by *P. amurensis,* summing net calcium carbonate production and respiration, for all sampling sites and years, was 55 (±51) g C m^{-2} yr^{-1}. The more saline regions of San Francisco Bay (San Pablo, Central, and South Bay; Fig. 1) are likely to have even higher rates of CO$_2$ production because of a higher dissolved calcium concentration and higher molluscan biomass, including populations of *P. amurensis* and four other introduced large bivalves: between 1994 and 1997, the seaward regions of San Francisco Bay had mean molluscan biomass 3–10 times higher than that measured in Suisun Bay (http://www.sfei.org/rmp/reports.htm#tr). Therefore, the rates of CO$_2$ production by *P. amurensis* in Suisun Bay (Table 2) are underestimates of the areal CO$_2$ production rate by all calcified organisms averaged over the entire San Francisco Bay ecosystem.

Annual primary production in Suisun Bay is ~20 g C m^{-2} yr^{-1} (Alpine and Cloern 1992) and would consume only 36% of the CO$_2$ produced by *P. amurensis.* This exotic clam is therefore a major source of CO$_2$ to northern San Francisco Bay. From monthly measurements of dissolved inorganic carbon concentration and pH in Suisun Bay during 1999–2000, the median computed pCO$_2$ was 583 μatm ($n = 16$; W. Sobczak pers. comm.). This degree of CO$_2$ supersaturation with respect to the atmosphere (~360 μatm) implies that, on average, the water column releases CO$_2$ to the atmosphere. Estuaries typically have supersaturated concentrations of dissolved CO$_2$ and are net sources of CO$_2$ to the atmosphere. For example, Frankignoulle et al. (1998) showed that nine European estuaries release 30–60 million tons of carbon per year to the atmosphere, which is equivalent to 5%–10% of present anthropogenic CO$_2$ emissions for all of Western Europe. Macrozoobenthic respiration and calcium carbonate production contribute to that emission: for the combined northern and southern San Francisco Bays (9.9 × 10^8 m^2), using the mean CO$_2$ production calculated here, the total CO$_2$ production by *P. amurensis* alone is 5.4 × 10^{10} g C yr^{-1}. However, not all of this clam-generated CO$_2$ is available for release to the atmosphere, because some (unmeasured) fraction is titrated to HCO$_3^-$ by internal sources of alkalinity such as sulfate reduction and denitrification. For example, Raymond et al. (2000) determined that 60% of the excess CO$_2$ produced in the York River Estuary evades to the atmosphere, and 40% is exported as HCO$_3^-$.

Our estimated mean carbonate production rate by *P. amurensis* in northern San Francisco Bay is much lower than rates reported in other estuaries for other calcareous organisms (Table 3). Therefore, an extrapolation of the mean calcification rate of *P. amurensis* to the world's estuaries should yield a lower limit to the estimated global strength of this CO$_2$ source. The total surface of estuaries is ~1.8 × 10^{12} m^2; calcareous organisms would therefore produce at least 4 × 10^{14} g CaCO$_3$ yr^{-1} within these ecosystems, equivalent to 44% of the CaCO$_3$ production rate by the world's coral reefs (Milliman 1993). If we extrapolate the total gross CO$_2$ production rate (respiration plus calcification) of *P. amurensis* in northern San Francisco Bay to the world estuaries, this source would produce 9.9 × 10^{13} g C yr^{-1} as CO$_2$ emitted to the water. Mollusks and other calcified organisms living on estuarine bottoms are therefore a significant CO$_2$ source, comparable in magnitude to the total emissions of CO$_2$ from the world's freshwater lakes (Cole et al. 1994) and from

volcanic-metamorphic fluxes of CO_2 (Brantley and Koepenick 1995) to the atmosphere.

Effects of other invasive alien calcareous species

We now have compelling evidence that bivalve mollusks strongly influence the cycling of carbon, nitrogen, phosphorus, sulfur, and silicon. Here, we show that an introduced mollusk can also markedly influence inorganic carbon cycling in San Francisco Bay by providing an important supply of CO_2 to the overlying waters. Calcification by benthic organisms has not been considered to be a source of CO_2 to lakes (Cole et al. 1994), rivers (Raymond et al. 1997), or estuaries (Frankignoulle et al. 1996). Computations of C budgets usually consider only respiration as an internal CO_2 source, even where the mollusk biomass is high. Should the zoobenthic calcification source also be included in inorganic C budgets, particularly for lakes and rivers where *D. polymorpha, C. fluminea,* or other exotic mollusks have proliferated enough to control primary production or deplete dissolved oxygen?

Direct measurements of both tissue and shell production have not been made for other invasive bivalve species, but we can estimate the total CO_2 generation rates by invasive bivalves where their biomass or tissue production has been measured. We used published biomass measurements of native bivalves (preinvasion) and *Dreissena* or *Corbicula* (postinvasion) in 6 freshwater systems where invasions and their ecological consequences have been followed. From measured biomass, we computed the minimum potential secondary production (P_{min}) for each bivalve species, using lower limits of published ratios of production (P) to biomass (B). We used P_{min} and the respiration equation of Schwinghamer et al. (1986) to compute the minimum CO_2 production rate from respiration (R_{min}). We also used P_{min} to compute the minimum CO_2 production rate from calcification (C_{min}), under the assumption that the ratio of shell ($CaCO_3$) production : tissue production equals the ratio of shell biomass : tissue biomass, as it does for *Potamocorbula*. These computations (Table 4) indicated that (1) the gross CO_2 production rate from calcification can be of comparable magnitude to that from respiration (the ratio varies with animal size and degree of calcification) and (2) massive invasions by *Dreissena* and *Corbicula* can increase, by up to two orders of magnitude, the total CO_2 production rate by the bivalve community, compared with preinvasion conditions. Our intent here is not to derive accurate estimates of CO_2 production rates from biomass measurements but rather to compute lower bounds on the potential CO_2 production rates by native and invasive bivalves. If we imagine an invasive mollusk species in all the world's rivers and lakes (200×10^{10} m^2) and use the mean total CO_2 production for invaded North American freshwater ecosystems considered here (533 g C m^{-2} yr^{-1}; Table 4), the potential gross CO_2 production is 1.06×10^{15} g C yr^{-1} (comparable to CO_2 fluxes from land-use changes of 1.1×10^{15} g C yr^{-1}; Schimel 1998).

Implications

Massive populations of invasive bivalves are developing throughout the world as a result of human introductions both

Table 4. Estimated minimum rates of CO_2 generation (all in g C m^{-2} yr^{-1}) by native and introduced bivalve mollusks in six North American freshwater ecosystems. Measured biomass was converted to g C m^{-2}, assuming C biomass = 0.41 × dry-weight biomass and dry-weight biomass = 0.04 × wet-weight biomass. Secondary production (P_{min}) was calculated from biomass using minimum $P:B$ ratios for each species or group: 0.2 for Unionidae, 4.5 for Sphaeridae, 4.45 for *Corbicula*, and 0.8 for *Dreissena* (McMahon 1999). The respiration rate (R_{min}) was computed from P_{min}, using the equation of Schwinghamer et al. (1986). Calcification (C_{min}) was computed from P_{min}, under the assumption that the ratio of shell production (g CaCO$_3$ m^{-2} yr^{-1}) : tissue production (g C m^{-2} yr^{-1}) = 10 for *Potamocorbula* (present study); 15 for *Corbicula* (Thompson unpubl. data), Unionidae, and Sphaeridae; and 7 for *Dreissena* (Dermott and Kerec 1997). Biomass measurements are from Miller et al. 1986 (Ohio River), Miller and Payne 1994, Effler and Siegfried 1994 (Seneca River); Nalepa et al. 1996 (Lake St. Clair; and Dermott and Kerec 1997 (Lake Erie). The production of *Corbicula* in Delta Mendota Canal was computed from size-frequency distributions (Eng 1977). The last column gives the estimated increase in CO_2 generation (g C m^{-2} yr^{-1}) after invasion by introduced bivalves. Detailed calculation methods are given in Web Appendix 1 at http://www.aslo.org/lo/toc/vol48/issue6/2086a1.pdf.

Location	Areal extent of study	Years	Native bivalves	B	P_{min}	R_{min}	C_{min}	CO_2 production	Years	Introduced bivalve	B	P_{min}	R_{min}	C_{min}	CO_2 production	Increase
Seneca River	16-km concrete canal	1993	None						1993	*Dreissena*	294	235	518	198	716	716
Lake St. Clair	Lake average	1986	Unionidae	1.8	0.4	0.8	0.7	1.5	1994	*Dreissena*	1	1	2	1	3	3
		1994	Unionidae	0	0			0								
Lake Erie	Profundal region (6% of lake area)	1979	Sphaeridae	0.0	0.1	0.1	0.1	0.2	1993	*Dreissena*	4	4	8	3	11	11
		1993	Sphaeridae	0.0	0.0	0.1	0.0	0.1								
Ohio River	Unionid habitat, 2 sites	1983	Unionidae	39	8	18	14	32	1983	*Corbicula*	62	278	611	500	1,111	1,079
Ohio River	Unionid habitat, 4.8 km	1983–1992	Unionidae	16	3	7	6	13	1983–1992	*Corbicula*	53	234	515	421	936	923
Delta Mendota	117-km concrete canal	1973–1974	None						1973–1974	*Corbicula*		105	233	189	422	422

deliberate and accidental (Strayer et al. 1999). Given their current scale, biotic invasions have taken their place within human-driven atmospheric (Walther et al. 2002) and aquatic alterations (Mack et al. 2000) as major agents of global change. When considering the impact of invasive calcareous zoobenthic species on the global carbon budget, this biogenic source of CO_2 is expected to increase in the future because (1) Ψ will increase by $\sim 12\%$ (Frankignoulle et al. 1994), for a doubling of the preindustrial atmospheric CO_2 level; (2) eutrophication can lead to an increase of mollusk biomass and increased CO_2 generation, because benthic production is stimulated by nutrient enrichment (Wollast 1994); (3) mollusk aquaculture production is growing rapidly in the world coastal zone, from 3.4×10^9 kg in 1988 to 10.7×10^9 kg in 2000 (FAO–Fisheries Department; http://www.fao.org/fi/statist/summtab/default.asp.); and (4) biological invasions will continue as expanding international commerce accelerates the translocation of fauna (Carlton and Geller 1993). The prominent invasive mollusks in freshwater (*D. polymorpha, C. fluminea,* and *Rangia cuneata*) and marine/estuarine ecosystems (*C. fornicata, Corbula gibba, Ensis directus, Littorina littorea, Maoricolpus roseus, Mytilopsis sallei, Mytilus galloprovincialis, Musculista senhousia, Ovatella myosotis, Perna viridis, Limnoperna fortunei,* and *Batillaria attramentaria*) continue to spread worldwide. Invasive alien organisms have become a key component of global change, threatening ecosystem functioning, biodiversity, species integrity, water availability, and the attractiveness of natural areas. Now we must also consider their previously unrecognized significance as a globally important potential source of $CaCO_3$ and CO_2.

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