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Shell growth rates of pteropod and heteropod molluscs and aragonite production in the open ocean: Implications for the marine carbonate system

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ABSTRACT

Shell calcification rates of four species of euthecosomatous pteropods and two species of shelled heteropods were measured in short-term ^{45}Ca uptake experiments. In subtropical, temperate, and subarctic waters of the North Pacific Ocean and Atlantic Ocean, animals were hand-collected by Scuba divers, captured with the use of a submersible and caught in plankton nets. Shell growth rates of pteropods ranged from 1.1 to 7.8 μg Ca deposited (mg Ca shell)$^{-1}$ h^{-1}. Heteropod growth rates ranged from 4.6 to 4.9 μg Ca deposited (mg Ca shell) $^{-1}$ h^{-1}.

Aragonite production of shelled pteropods and heteropods at stations in the eastern Equatorial Pacific, North Pacific Central Water and the Tongue of the Ocean, Bahamas, was estimated using the instantaneous growth rate method. At all stations, pteropods were 3 to 9 times more abundant than heteropods and constituted 65 to 96% of aragonite production. Estimates of aragonite production ranged from 2.1 to 6.9 mg $CaCO_3$ m^{-2} d^{-1}. Using weighted averages based on two broad divisions of oceanic productivity, results were compared to reported aragonite fluxes measured with sediment traps. The data indicate that a source of alkalinity other than the dissolution of pteropod and heteropod aragonite is needed to supply the majority of a published estimate of $CaCO_3$ dissolution in the water column of the North Pacific.

1. Introduction

Shelled pteropods (Opisthobranchia: Euthecosomata) and heteropods (Prosobranchia: Mesogastropoda) are the principal pelagic producers of aragonite, a form of calcium carbonate ($CaCO_3$) that is about 50% more soluble in seawater than calcite (Mucci, 1983), the $CaCO_3$ polymorph precipitated by foraminifera and coccolithophorids. Unlike the calcite skeletons of foraminifera and coccolithophorids, all of the aragonite shells produced by pteropods and heteropods in more than 98% of oceanic regions dissolve while sinking through the water column or upon reaching the ocean floor (Berger, 1978; Byrne *et al.*, 1984). Dissolution of sinking aragonite tests has been suggested as the source of unusual alkalinity maxima that occur at midwater depths in

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the North Pacific (Berner, 1977; Fiadeiro, 1980a, b; Betzer *et al.*, 1984). Moreover, because of the high solubility of aragonite compared to calcite, pteropod and heteropod shells may be important in the first stages of oceanic neutralization of fossil fuel carbon dioxide (CO_2) (Berner and Honjo, 1981; Whitfield, 1984).

Recent results of sediment trap studies suggest that aragonite constitutes a minimum of 12% of total $CaCO_3$ flux (Berner and Honjo, 1981), and may exceed the calcite flux of foraminifera by a factor of 5 (Betzer *et al.*, 1984). However, sediment traps may underestimate aragonite flux because of dissolution of aragonite when traps are deployed in undersaturated waters (Berner and Honjo, 1981; Betzer *et al.*, 1984), which typically occur below 200–600 m in the North Pacific Ocean and 1000–3800 m in the Atlantic Ocean (Li *et al.*, 1969; Feely *et al.*, 1984, 1988). Conversely, the capture of live pteropods in traps deployed in the generally supersaturated waters of the upper ocean can overestimate aragonite flux (Harbison and Gilmer, 1986). Thus, the quantitative significance of aragonite in the $CaCO_3$ cycle remains unresolved.

Another method of assessing the importance of planktonic molluscs to the carbonate system involves estimating their $CaCO_3$ production as shell growth. The secondary production of pteropods and heteropods measured in terms of $CaCO_3$ is an estimate of pelagic aragonite production. An unknown precentage of aragonite production is regenerated in the upper water column through grazing or dissolution in waters undersaturated with aragonite. Thus, total $CaCO_3$ production differs from the sinking carbonate flux collected with sediment traps, which can be viewed as net production.

In this report, I present the first direct measurements of growth rates of shelled pteropod and heteropod molluscs using short-term, ^{45}Ca uptake experiments. Estimates of oceanic aragonite production by pteropods and heteropods are calculated for three sampling stations, and implications for the marine carbonate system are discussed.

2. Methods

a. Growth rates

Shell growth rates were measured for four species of euthecosomatous pteropods and two species of heteropods collected from shallow depths (5 to 30 m) in the North Pacific Ocean and the Atlantic Ocean, using ^{45}Ca as an index of calcification. Sampling dates, locations, and water temperatures are listed in Table 1. Animals were hand-collected by Scuba divers, with the exception of the pteropod *Cavolinia uncinata,* which was captured in collecting jars mounted to the front of the submersible, the Johnson Sea-Link. Additionally, to test for differences in the calcification rates of diver-collected pteropods versus net-collected pteropods, specimens of *Clio pyramidata* were collected concurrently by divers and with a 1-m plankton net tow of short duration.

All experimental chambers were 1-liter, opaque, polyethylene jars. Prior to use, jars

Table 1. Instantaneous growth rates ± 1 standard error for shelled pteropods and heteropods.

Species	Temperature (°C)	Collection Station	Date	Growth Rate* (μg Ca deposited/ mg Ca shell/h) (n)	Shell Weight* (mg)	Mean Isotopic Exchange† (% of total activity)
Pteropods						
Clio pyramidata	11	Subarctic Pacific 50N; 145W	7/18/86	1.1 ± 0.1 (7)	2.06 ± 0.28	20
Cavolinia tridentata	17	Central Pacific 38N; 151W	7/9/85	7.7 ± 0.5 (12)	1.64 ± 0.34	22
Cavolinia uncinata	25	Bahamas 25N; 78W	10/18/86	2.9 ± 0.6 (9)	3.48 ± 0.47	15
Creseis virgula virgula	18	Santa Barbara Channel 34°23'N; 119°50'W	9/9/87	7.6 ± 0.8 (22)	0.20 ± 0.02	32
Heteropods						
Carinaria japonica	14	Central Pacific 42N; 149W	7/11/85	4.6 ± 0.4 (6)	9.02 ± 1.95	15
Atlanta sp.	18	Santa Barbara Channel 34°23'N; 119°50'W	9/18/87	4.9 ± 0.5 (9)	0.16 ± 0.02	35

*Mean ± 1 standard error

†Calculated from shells of dead animals processed with experimental animals

were rigorously cleaned (Fitzwater *et al.*, 1982). One to 6 animals were captured in each jar by divers, or transferred to jars from net or submersible collections. Jars were immediately placed in a water bath maintained at the temperature at which the animals were collected. To differentiate the isotopic exchange of ^{45}Ca from the biological uptake of ^{45}Ca, shells of animals collected in plankton tows and subsequently frozen were also placed in jars and handled in the same manner as experimental animals. These control shells were of the same size and species as those of experimental animals. Animal tissues of control shells were either removed or had withdrawn deep inside the shell, possibly exposing a greater shell surface area to incubation seawater than the shells of living animals. $^{45}CaCl_2$ was added to each jar to obtain an initial activity of 0.3 μCi ml^{-1}. At several intervals during each experiment, animals were individually removed from jars, rinsed with ethanol, and dropped into a vial of ethanol heated to 60°C.

In the laboratory, pteropods and heteropods were dried and weighed on a Cahn electrobalance, Model 4600. Each shell was dissolved with 0.5 N HCl and the solution was neutralized with 0.1 N NaOH. The remaining tissue was quantitatively rinsed with deionized water and removed.

Two replicates of dissolved shell solution were analyzed for ^{45}Ca activity using a LKB-Wallac 1217 Rackbeta liquid scintillation counter. The ^{45}Ca activity of each shell at the termination of incubation was calculated using a decay constant of 4.2×10^{-3} disintegrations per day.

A third aliquot of dissolved shell solution was analyzed for total calcium concentration using a Varian Model 6 flame atomic absorption spectrophotometer. Potassium chloride was added to samples, standards, and blanks to suppress ionic interferences, and a nitrous oxide-acetylene flame was used for all analyses.

The amount of calcium deposited during each experiment was standardized to the total calcium content of the shell and calculated from the equation:

$$D = \frac{(S_{cpm}/W_s) - (C_{cpm}/W_c)}{I_{cpm}} * K \tag{1}$$

where D is the calcium deposition in μg Ca deposited per mg Ca shell, S_{cpm} and C_{cpm} are the counts per minute of the experimental shell and control shell, W_s and W_c are the calcium content in mg of the experimental shell and control shell, I_{cpm} is the activity in counts per minute of 1 ml of the incubation water at the start of the experiment, and K is the concentration of calcium in seawater (412 μg Ca ml^{-1} (Bruland, 1983)).

b. Production

To provide a preliminary assessment of the aragonite fraction of total pelagic $CaCO_3$ production, the aragonite production of shelled pteropods and heteropods in three oceanic regions was estimated by the instantaneous growth rate method (reviewed in Waters, 1977; Benke, 1984). Standing stocks of pteropods and heteropods were

sampled at stations in the eastern Equatorial Pacific, the North Pacific Central Water, and the Tongue of the Ocean, Bahamas, using quantitative, oblique plankton tows from a maximum depth of 250 m to the surface. Collection stations for biomass samples were sometimes different than sampling sites for growth experiments. Sampling locations, depths, and dates are listed in Table 2. All tows were conducted with nets of 73 μm or 150 μm mesh at night when pteropods and heteropods are concentrated in the upper water column (Wormuth, 1981; Seapy, 1987, 1988). Plankton samples were preserved with 4% formalin in seawater buffered with sodium borate (pH 8.2). Samples were divided with a Folsom plankton splitter to $1/2$, $1/4$ or $1/8$ of the original sample. Subsamples of at least 600 pteropods and heteropods were counted under a microscope at 250× magnification. More than 100 individuals per station were randomly chosen for shell weight determinations. Animal tissues inside shells were digested in a solution (2:1 by volume) of 0.1 N NaOH and 30% H_2O_2 at 50°C for 24–48 h. Empty shells were rinsed with ethanol, dried and weighed. The average pteropod or heteropod shell weight was calculated and multiplied by the numerical abundance of pteropods or heteropods in the sample to obtain the $CaCO_3$ biomass of each group.

The aragonite production of pteropods and heteropods respectively was calculated from the equation:

$$P = GB \tag{2}$$

where P is the production (mg $CaCO_3$ m^{-2} d^{-1}), G is the average instantaneous growth rate (mg $CaCO_3$ deposited (mg $CaCO_3$ shell)$^{-1}$ d^{-1}) calculated separately for pteropods and heteropods from results of the ^{45}Ca uptake experiments, and B is the $CaCO_3$ biomass (mg $CaCO_3$ m^{-2}) of each group determined from plankton tows. Standard errors for production estimates were calculated by propagating errors associated with growth rates and, when determined from more than one plankton tow, carbonate biomass (Bevington, 1969).

3. Results

a. Growth rates

Shell growth rates of the six pteropod and heteropod species ranged from 1.1 to 7.7 μg Ca deposited (mg Ca shell)$^{-1}$ h^{-1} (Table 1). Animals collected for growth experiments were small to medium-sized individuals, generally in the middle of the size range of each species (van der Spoel, 1967, 1976); neither veligers nor large individuals were used in experiments. Mean shell growth rates (± S.E.) measured for the four pteropod species and two heteropod species were 4.8 ± 0.5 and 4.7 ± 0.4 μg Ca deposited (mg Ca shell)$^{-1}$ h^{-1}, respectively (Table 1, Figs. 1, 2).

Isotopic exchange measured in control shells was subtracted from the total ^{45}Ca activity of experimental shells to obtain rates of shell deposition. During the first hour

Table 2. Abundance, calcium carbonate biomass and production of shelled pteropods and heteropods sampled at 3 regions. Oblique plankton tows for biomass estimates were conducted at night from 150-0 m at the Bahamas station, 250-0 m at the equatorial Pacific station, and 200-0 m at stations in the Central Pacific. Production estimates were calculated by the instantaneous growth rate method using mean rates of shell deposition measured for pteropods and heteropods. Values are reported with ± 1 standard error.

Station	Date	Net Mesh (μm)	No. of Tows	Abundance Pteropod (No. m^{-3})	Abundance Heteropod (No. m^{-3})	$CaCO_3$ Biomass Pteropod (mg m^{-2})	$CaCO_3$ Biomass Heteropod (mg m^{-2})	$CaCO_3$ Production Pteropod (mg $m^{-2}d^{-1}$)	$CaCO_3$ Production Heteropod (mg $m^{-2}d^{-1}$)
Bahamas 25°21′N; 77°54′W	19 Oct 1986	73	1	9.7	2.7	24.4	1.4	2.8 ± 0.3	0.2 ± 0.1
Equatorial Pacific 0 50′N; 86W	13–18 Mar 1985	150	3	53.6 ± 8.8	6.3 ± 1.6	56.7 ± 7.6	2.6 ± 0.9	6.6 ± 1.2	0.3 ± 0.1
Central Pacific 29°40′N; 134°52′W 28°28′N; 139°6′W	17–19 July 1983	150	3	29.7 ± 6.8	9.0 ± 1.5	11.9 ± 2.7	5.8 ± 0.9	1.4 ± 0.6	0.7 ± 0.2

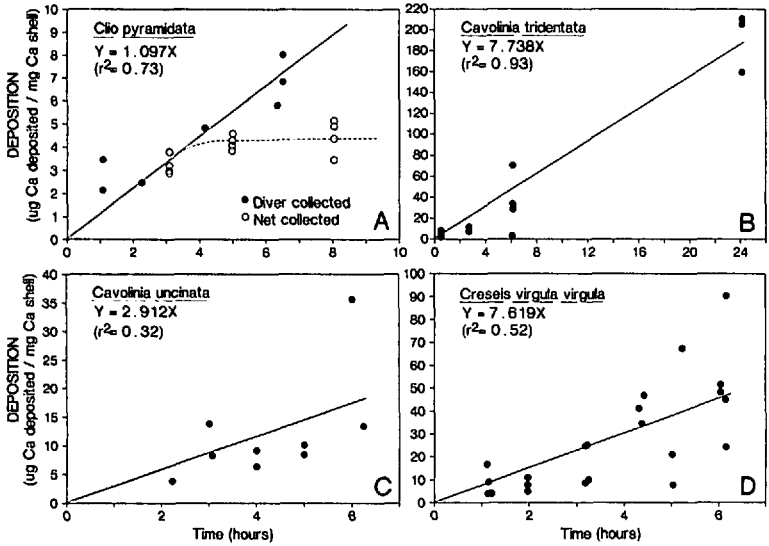

Figure 1. Rate of calcium deposition in pteropod shells as measured by ^{45}Ca uptake. Each point represents one animal. In all regressions, the coefficient was significantly different from zero ($P < 0.05$, t test). (a) *Clio pyramidata.* Squares are diver-collected animals and pluses are net-collected animals. (b) *Cavolinia tridentata.* (c) *Cavolinia uncinata.* (d) *Creseis virgula virgula.*

of each experiment, isotopic exchange of ^{45}Ca accounted for a substantial fraction of the total radioactivity (24–70%). Exchange decreased to 1–13% of total radioactivity in shells incubated for 6 hours or longer. Shell deposition rates are probably conservative because isotopic exchange rates determined from shells of dead animals were likely overestimates, resulting from the larger surface area exposed in exchange shells compared to those of living animals.

Comparison of diver-collected and net-collected specimens of *Clio pyramidata* (Fig. 1a) reveals that the calcification rate of net-collected animals leveled off after about 3 h, while calcification continued to increase linearly in diver-collected animals.

A plot of shell deposition rate versus time for the heteropod *Carinaria japonica* revealed a decrease in calcification for animals incubated 24 hours, probably as a result of stress from captivity and starvation. Thus, only animals in the first 12 hours of the experiment were included in the determination of growth rate (Fig. 2a). Specimens of *Cavolinia tridentata* were also incubated for 24 hours, but no decrease in calcification was noted under these laboratory conditions. The *Carinaria* specimens were much larger, and may have been more physically confined than the *Cavolinia tridentata* specimens.

Although one might expect smaller and presumably younger animals to calcify at a faster rate than larger animals of the same species, the rate of shell deposition was

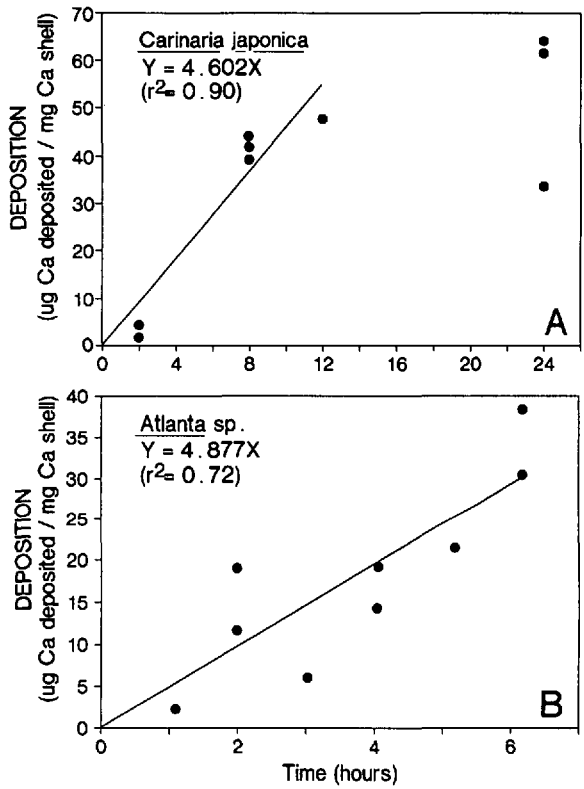

Figure 2. Rate of calcium deposition in heteropod shells as measured by ^{45}Ca uptake. Each point represents one animal. In both regressions, the coefficient was significantly different from zero ($P < 0.05$, t test). (a) *Carinaria japonica.* Because a plot of shell deposition versus time indicated a decrease in calcification for animals incubated for 24 h, the points at 24 h were not used to calculate the regression. (b) *Atlanta* sp. (R. R. Seapy, personal communication).

significantly correlated with shell weight in only one species, *Creseis virgula virgula* ($P < 0.05$, t test). The logarithmic relationship between shell deposition and shell weight was not significant ($P > 0.05$, t test) for any species.

b. Production

Abundance, $CaCO_3$ biomass and production for shelled pteropod and heteropod populations in each of the three regions sampled are listed in Table 2. Pteropods were 3 to 9 times more abundant than heteropods. Heteropods accounted for a small fraction (4–7%) of the aragonite production at the Bahamas and Equatorial Pacific sites, and 35% of aragonite production in the Central Pacific. Total aragonite production of pteropods and heteropods ranged from 2.1 to 6.9 mg $CaCO_3$ m^{-2} d^{-1}. Aragonite production was greatest at the Equatorial Pacific station and lowest in the Central Pacific, consistent with patterns of primary production in these regions.

4. Discussion

a. Growth rates

Shell growth rates measured in this study are the first direct measurements of pteropod and heteropod growth. Shell deposition is related to the total weight growth, although the relationship between shell weight and tissue weight is not necessarily linear. For *Clio pyramidata* in the subarctic Pacific, for example, the logarithmic relationship between shell weight and tissue weight is curvilinear (Fabry, 1989). Because euthecosomatous pteropods do not produce feeding webs in the laboratory and presumably do not feed, only short-term growth experiments, such as the ^{45}Ca uptake studies presented here, are possible. Shell deposition rates measured in this study are probably conservative, owing to the stress associated with capture and confinement, and because rates of isotopic exchange used in calculations may have been overestimates. However, in the extreme and unlikely case that no isotopic exchange occurred in shells of living animals, the average increase in growth rates would be only 14%.

Although plankton nets are convenient and easily collect large numbers of animals, nets damage pteropods. Use of net-collected pteropods in growth experiments would result in underestimated growth rates. Collection by Scuba divers provides undamaged specimens, but frequently in this study, only a limited sample size was available.

Earlier workers estimated an increase in mean shell length or diameter of 0.1 to 0.3 mm per month in several pteropod species collected in time-series plankton samples (Redfield, 1939; Kobayashi, 1974; Wells, 1976). However, because the relationship between shell size and shell weight is not known for those species, the growth rates expressed in terms of shell mass in this study cannot be readily compared with results of previous work. Moreover, some pteropod species, including those in the genus *Cavolinia*, do not continually increase shell length or width during development. As adults, these species only increase the thickness of the shell wall (Bé *et al.*, 1972). Therefore, linear dimensions are not reliable measures of shell growth for all pteropod species.

b. Production

Estimates of daily aragonite production reported here are approximate for two reasons. First, I assumed that the growth rate of pteropods and heteropods does not vary with animal size. This assumption is supported by the observation that, within the size range of animals used in ^{45}Ca experiments, shell growth rate did not vary with shell size in all but one pteropod species. Moreover, Wells (1976) found no significant difference in the shell growth rates of small and large sizes of any of the four pteropod species he examined. Secondly, pteropods and heteropods were treated as two groups in production calculations, with no differentiation among species. Shell calcification rates for the pteropod and heteropod species investigated were all of the same order of magnitude, however, even though animals were collected from different oceanic

regions and experiments were conducted at different water temperatures. Hence, use of mean growth rates in production estimates is a reasonable approximation.

Pteropod abundances measured in this study are consistent with or higher than densities reported for similar oceanic regions (eg., McGowan, 1960; Berger, 1971; Wells, 1978; Wormuth, 1981), but are an order of magnitude less than swarm densities that have occasionally been recorded (McGowan, 1967; Sakthivel and Haridas, 1974; Wormuth, 1981). No data on heteropod abundances in my sampling regions are available for comparison.

Turnover time, defined as the length of time required to replace the biomass of the population (reviewed in Benke, 1984), can be calculated from the ratio of biomass to production. At the three stations sampled, turnover times range from 8.4 to 8.7 days for pteropods and from 7.0 to 8.4 days for heteropods. These turnover times are consistent with turnover times estimated for other zooplankton species at low and mid latitudes (reviewed in Tranter, 1976).

Several sediment trap studies have estimated mass fluxes of aragonite at various locations (Honjo, 1978; Berner and Honjo, 1981; Betzer *et al.*, 1984). Sediment trap values of aragonite flux will be less than total production if aragonite dissolves in the water column above the sediment trap, either through biological transformations or in waters undersaturated with respect to aragonite, or if aragonite collected in sediment traps dissolves before the sample is recovered.

In Table 3, values in the literature of aragonite mass flux measured with sediment traps are compared to aragonite production estimated from the secondary production of pteropods and heteropods. To avoid possible inclusion of live pteropods, only flux estimates from traps suspended below the typical vertical range of pteropods (upper 600 m) were used. Additionally, data from traps deployed high in the water column, but below 600 m, were chosen over traps deployed in deep waters in an effort to reduce the amount of aragonite lost through dissolution in the water column.

Although the data base is small, general estimates of aragonite production and flux can be obtained by weighting the measurements according to regional productivity. The three oceanic provinces recognized by Ryther (1969) were condensed to two divisions: (i) open ocean, covering 90% of the ocean area, and (ii) coastal and upwelling areas, composing the remaining 10% of the ocean surface. Seasonal variation was not considered in the analysis. For the data sets in Table 3, the weighted average of aragonite production (2.9 mg $CaCO_3$ m^{-2} d^{-1}) exceeds the weighted average of aragonite flux (2.4 mg $CaCO_3$ m^{-2} d^{-1}) by a factor of 1.2. By comparison, the unweighted average of these aragonite production values is 4.1 mg $CaCO_3$ m^{-2} d^{-1}, 60% more than the unweighted average of aragonite flux estimates (2.6 mg $CaCO_3$ $m^{-2}d^{-1}$).

c. Aragonite production and the marine carbonate system.

Anomalous alkalinity maxima observed at intermediate depths in the North Pacific have been attributed to the dissolution of pteropod aragonite in the water column

Table 3. Comparison of aragonite production, estimated as the secondary production of pteropods and heteropods sampled in night plankton tows, and reported values of aragonite flux measured with sediment traps. Weighted averages are based on two divisions of oceanic productivity from Ryther (1969): open ocean (90% of ocean area) and coastal and upwelling areas (10% of ocean area).

Location	Position	Date	Depth (m)	$CaCO_3$ (mg m^{-2} d^{-1})	Reference
Secondary Production					
*Bahamas	25N 77W	10/86	0-150	3.0	This study
Equatorial Pacific	0N 86W	3/85	0-250	6.9	This study
*Central Pacific	29N 134W 28N 139W	7/83	0-250	2.1	This study
Subarctic Pacific	50N 145W	6/85	0-250	4.4	Fabry, 1989
			UNWEIGHTED AVERAGE =	4.1	
			WEIGHTED AVERAGE =	2.9	
Sediment Traps					
Panama Basin	5N 81W	7/79–11/79	677	5.4	Berner and Hongo, 1981
*Equatorial Atlantic	13N 54W	11/77–2/78	988	3.4	Berner and Honjo, 1981
*North Pacific	16N 165E	5/82	900	1.4	Betzer *et al.*, 1984
*North Pacific	21N 165E	6/82	900	1.7	Betzer *et al.*, 1984
*North Pacific	26N 165E	6/82	900	0.1	Betzer *et al.*, 1984
*North Pacific	30N 165E	6/82	900	1.0	Betzer *et al.*, 1984
*North Pacific	34N 165E	6/82	900	6.5	Betzer *et al.*, 1984
North Pacific	49N 165E	6/82	900	1.0	Betzer *et al.*, 1984
			UNWEIGHTED AVERAGE =	2.6	
			WEIGHTED AVERAGE =	2.4	

*denotes open ocean

(Berner, 1977; Betzer *et al.*, 1984; Byrne *et al.*, 1984). From examination of GEOSECS alkalinity data and an analysis of alkalinity distributions with a three-dimensional model, Fiadeiro (1980a,b) estimated a mean $CaCO_3$ dissolution rate in the North Pacific of 40 mg $CaCO_3$ m^{-2} d^{-1}, of which at least 35 mg $CaCO_3$ m^{-2} d^{-1} must be evenly distributed throughout the water column. While dissolution of pteropod and heteropod aragonite undoubtedly contributes to the excess alkalinity found at midwater depths in the North Pacific, these results indicate that the pteropod and heteropod contribution of 2.9 mg $CaCO_3$ m^{-2} d^{-1} is sufficient to account for only 8% of the calculated rate of $CaCO_3$ dissolution.

It is important to recognize that the aragonite production values reported here are instantaneous measurements, whereas calculated $CaCO_3$ dissolution rates are based on processes that occur over several tens to hundreds of years. An indication of the long-term variation of pteropod production may be obtained from the sediment trap study of Almogi-Labin *et al.* (1988), which computed the numerical flux of pteropods in a series of 19 samples collected over 4 years in the Sargasso Sea. During the 4-year period of continuous sampling, the average flux of pteropods was 250 specimens m^{-2} d^{-1}; the highest value measured was 3 times greater than the mean and the lowest value was 0.3 of the mean. If the long-term variation of the aragonite production measured here is similar to the range of pteropod fluxes reported by Almogi-Labin *et al.* (1988), pteropod and heteropod aragonite production could constitute 3–30% of the calculated rate of $CaCO_3$ dissolution in the North Pacific. Additional information on the seasonal and interannual variations in pelagic aragonite production is needed, but the current data indicate that a source of alkalinity other than pteropod dissolution is required to supply the majority of the estimated $CaCO_3$ dissolution in the North Pacific.

Although the alkalinity maxima in the North Pacific occur at depths where little dissolution of calcite would be expected from consideration of the carbonate chemistry of the water column, calcite could dissolve through biological transformations, as suggested by Fiadeiro (1980b). Possible mechanisms include digestion in the guts of animals and dissolution in oxygen-depleted zones that have been measured around and within fecal pellets and marine snow particles (Alldredge and Cohen, 1987).

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REFERENCES

Alldredge, A. L. and Y. Cohen. 1987. Can microscale chemical patches perist in the sea? Microelectrode study of marine snow, fecal pellets. Science, *235*, 689–691.

Almogi-Labin, A., Ch. Hemleben and W. G. Deuser. 1988. Seasonal variation in the flux of euthecosomatous pteropods collected in a deep sediment trap in the Sargasso Sea. Deep-Sea Res., *35*, 441–464.

Bé, A. W. H., C. MacClintock and D. C. Currie. 1972. Helical shell structure and growth of the pteropod *Cuvierina columnella* (Rang) (Mollusca, Gastropoda). Biomineralization Res. Rep., *4*, 47–79.

Benke, A. C. 1984. Secondary production of aquatic insects, *in* The Ecology of Aquatic Insects, V. H. Resh and D. M. Rosenberg, eds., Praeger, NY, 289–322.

Berger, W. H. 1971. Planktonic foraminifera: sediment production in an oceanic front. J. Foramin. Res., *1*, 95–118.

—— 1978. Deep-sea carbonate: pteropod distribution and the aragonite compensation depth. Deep-Sea Res., *25*, 447–452.

Berner, R. A. 1977. Sedimentation and dissolution of pteropods in the ocean, *in* The Fate of Fossil Fuel CO_2 in the Oceans, N. R. Andersen and A. Malahoff, eds., Plenum Press, NY, 243–260.

Berner, R. A. and S. Honjo. 1981. Pelagic sedimentation of aragonite: its geochemical significance. Science, *211*, 940–942.

Betzer, P. R., R. H. Byrne, J. C. Acker, C. S. Lewis, R. R. Jolley and R. A. Feely. 1984. The oceanic carbonate system: a reassessment of biogenic controls. Science, *226*, 1074–1077.

Bevington, P. R. 1969. Data Reduction and Error Analysis for the Physical Sciences. McGraw-Hill, San Francisco, 336 pp.

Bruland, K. W. 1983. Trace elements in sea-water, *in* Chemical Oceanography, *8*, J. P. Riley and R. Chester, eds., Academic Press, NY, 157–220.

Byrne, R. H., J. G. Acker, P. R. Betzer, R. A. Feely and M. H. Cates. 1984. Water column dissolution of aragonite in the Pacific Ocean. Nature, *312*, 321–326.

Fabry, V. J. 1989. Aragonite production by pteropod molluscs in the subarctic Pacific. Deep-Sea Res., *36*, 1735–1751.

Feely, R. A., R. H. Byrne, J. G. Acker, P. R. Betzer, C.-T. A. Chen, J. F. Gendron and M. F. Lamb. 1988. Winter-summer variations of calcite and aragonite saturation in the northeast Pacific. Mar. Chem., *25*, 227–241.

Feely, R. A., R. H. Byrne, P. R. Betzer, J. F. Gendron and J. G. Acker. 1984. Factors influencing the degree of saturation of the surface and intermediate waters of the North Pacific Ocean with respect to aragonite. J. Geophys. Res., *89*, 10631–10640.

Fiadeiro, M. 1980a. Carbon cycling in the ocean, *in* Primary Productivity in the Sea, P. G. Falkowski, ed., Plenum Press, NY, 487–496.

—— 1980b. The alkalinity of the deep Pacific. Earth Planet. Sci. Letts., *49*, 499–505.

Fitzwater, S. E., G. A. Knauer and J. H. Martin. 1982. Metal contamination and its effect on primary production measurement. Limnol. Oceanogr., *27*, 544–551.

Harbison, G. R. and R. W. Gilmer. 1986. Effects of animal behavior on sediment trap collections: implications for the calculation of aragonite fluxes. Deep-Sea Res., *33*, 1017–1024.

Honjo, S. 1978. Sedimentation of materials in the Sargasso Sea at a 5,367 m deep station. J. Mar. Res., *36*, 469–492.

Kobayashi, H. A. 1974. Growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella* ("*Limacina*") *helicina* in the central Arctic Ocean. Mar. Biol., *26*, 295–301.

Li, Y.-H., T. Takahashi and W. S. Broecker. 1969. Degree of saturation of $CaCO_3$ in the oceans. J. Geophys. Res., *74,* 5507–5525.

McGowan, J. A. 1960. The systematics, distribution and abundance of the Euthecosomata of the North Pacific. Ph.d dissertation, University of California, San Diego, 212 pp.

—— 1967. Distributional atlas of pelagic molluscs in the California Current region. CalCOFI Atlas No. 6, State of California Marine Research Committee, 218 pp.

Mucci, A. 1983. The solubility of calcite and aragonite in seawater at various salinities, temperatures and one atmosphere total pressure. Amer. J. Sci., *283,* 780–799.

Redfield, A. 1939. History of a population of *Limacina retroversa* during the drift across the Gulf of Maine. Biol. Bull., *76,* 26–47.

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science, *166,* 72–76.

Sakthivel, M. and P. Haridas. 1974. Synchronization in the occurrence of *Trichodesmium* bloom and swarming of *Creseis acicula* Rang (Pteropoda) and *Penilia avirostris* Dana (Cladocera) in the area of Cochin. Mahasagar Bull. Nat. Inst. Oceanogr., *7,* 61–67.

Seapy, R. R. 1987. The heteropod fauna of oceanic waters off Hawaii. Western Society of Malacologists, Annual Report, *19,* 9–12.

—— 1988. Atlantid heteropods of Hawaiian waters. Western Society of Malacologists, Annual Report, *20,* 28–29.

Spoel, S. van der. 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda). J. Noorduijn en Zoon N. V. Gorinchem, 375 pp.

—— 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda). Bohn, Scheltema & Holkema, Utrecht, 484 pp.

Tranter, D. J. 1976. Herbivore production, *in* The Ecology of the Seas, D. H. Cushing and J. J. Walsh, eds., W. B. Saunders Co. Philadelphia, 186–224.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecological Res., *10,* 91–165.

Wells, F. E. 1976. Growth rates of four species of euthecosomatous pteropods occurring off Barbados, West Indies. The Nautilus, *90,* 114–116.

—— 1978. Seasonal patterns of abundance and reproduction of euthecosomatous pteropods off Barbados, West Indies. The Veliger, *18,* 241–248.

Whitfield, M. 1984. Surprise from the shallows. Nature, *312,* 310.

Wormuth, J. H. 1981. Vertical distribution and diel migrations of Euthecosomata in the northwest Sargasso Sea. Deep-Sea Res., *28A,* 1493–1515.

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