that occurred several delay times before the present.

The oscillatory nature of the solutions persists for fairly wide ranges of the various parameters. Changes in t_d and t_c only affect the frequency of $\overline{\theta}(t)$. The second term inside the pointed brackets in Eq. 2 is a positive number because the albedo feedback at high latitudes is larger than the average value. The oscillation tends to become more and more damped as this term is made smaller, but the solution retains its basic oscillatory character even when this term is set equal to zero (*6*).

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6. We are presently studying a more complex model in which sinking and upwelling can occur at several locations and in which the several deepwater currents can communicate with each other as well as with the surface layer.
7. The original idea for this word came while one of us (R.G.W.) was at the Institute for Energy Analysis, Oak Ridge, Tenn., in 1976. We thank Drs. Ralph Rotty and Alvin Weinberg for their hospitality. This work is supported by NSF grant ATM-7916332.

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Biological Control of the Removal of Abiogenic Particles from the Surface Ocean

Abstract. *Concurrent measurements of particle concentrations in the near-surface water and of particle fluxes in the deep water of the Sargasso Sea show a close coupling between the two for biogenic components. The concentrations of suspended matter appear to follow an annual cycle similar to that of primary production and deepwater particle flux. Although the concentration of particulate aluminum in the surface water appears to vary randomly with respect to that cycle, the removal of aluminum to deep water is intimately linked to the rapid downward transport of organic matter.*

For the past 4 years we have continuously sampled the flux of particles to the deep Sargasso Sea at a site 45 km southeast of Bermuda (32°05′N, 64°15′W). Samples were recovered bimonthly from a sediment trap moored 3200 m below the surface and 1000 m above the sea floor (*1*). We have observed quite reproducible annual fluctuations in the total particle flux with a maximum range of a factor of 7 among sampling periods but generally less than that within 1 year. Quite similar fluctuations were observed in individual major constituents, such as organic carbon and calcium carbonate. We soon recognized a similarity between the timing and extent of these variations and the seasonal changes in primary production in the Sargasso Sea as reported by Menzel and Ryther 20 years earlier (*2*): highs in early spring and lows in late summer and fall. Not surprisingly, these seasonal changes affect the flux of such biologically important elements as calcium, because the production of coccoliths and foraminiferal tests (*3*) is closely linked to the cycle of photosynthetic carbon fixation. We were surprised, however, to find that the flux of particulate aluminum in the deep water also undergoes annual variations (*4*) and is, in fact, quite closely correlated to the flux of organic carbon (Fig. 1).

By a combination of scanning electron microscopy and energy-dispersive x-ray spectrometry, we determined that aluminum in the sediment-trap material is primarily associated with clay particles or at least with apparently nonbiogenic, silicon-containing particles. Similar aluminum-containing particles were identified in the suspended load of the surface water. Some silicon-aluminum spherules, most likely fly-ash particles (mullite) from industrial coal combustion (*5*), were also identified in the sediment-trap material. Deuser *et al.* had proposed (*4*) that the seasonal cycle of the aluminum flux and the close correlation of aluminum with organic carbon in the sediment-trap samples might be caused by biological removal of the clay particles from the surface water. Deuser *et al.* suggested that the subsequent rapid sinking of the particles could be accomplished as a result of their association with fecal pellets or other organic aggregates. It was not known, however, if by coincidence the input of clay to the surface water might also have an annual cycle similar to that of primary production.

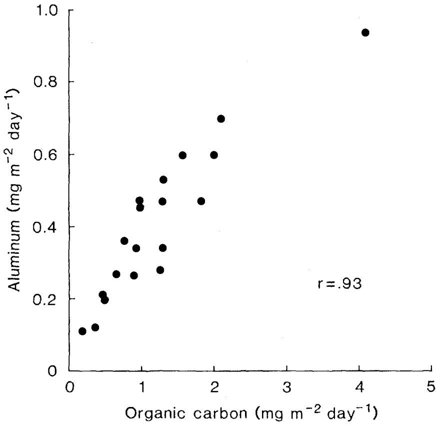

Fig. 1. Correlation between the fluxes of organic carbon and mostly abiogenic aluminum into a sediment trap at a depth of 3200 m in the Sargasso Sea. Points represent averages over 2-month collection periods between April 1978 and April 1982. Carbon and aluminum analyses were made on the < 37-μm fraction (after sieving) of material collected in the traps.

In order to obtain a measure of the particle input to, and formation in, the surface water, we subsequently began periodic sampling of the suspended matter in the top 200 m of the Sargasso Sea at a site near the sediment trap while also continuing the sediment-trap collections. Details of the sediment trap have been given in (*3, 4, 6*). Suspended matter was collected in 10- and 30-liter Niskin bottles, the contents of which were passed through Nuclepore filters (0.6-μm pore size) into evacuated carboys immediately upon arrival on deck. Depending on the suspended load, 2.5 to 12.5 liters passed through the filters before they became clogged. The calcium and aluminum concentrations in the material on the filters and in the < 37-μm size fraction of the sediment-trap samples were determined by instrumental neutron activation analysis (*7*). Samples were irradiated at the Rhode Island Nuclear Science Center in a neutron flux of 4×10^{12} neutron cm^{-2} sec^{-1} for 10 minutes and cooled for 5 minutes before counting on a Ge(Li) detector. We report here the results of the first year of concurrent measurements on suspended matter and sediment-trap samples.

For a comparison of the continuous flux measurements with the periodic concentration measurements we show on the left side of Fig. 2 juxtaposed plots of (i) the midpoints of seven 2-month sediment-trap accumulations, expressed as daily flux per square meter, and (ii) average suspended-matter concentrations in the surface water (sampling depths of 10, 25, 50, and 100 m) on 11 occasions between 9 April 1981 and 2 April 1982. The sediment-trap samples represent the particle accumulations during 99 percent of the time between 5 February 1981 and 6 April 1982 (421 of 425 days). The average interval between surface-water samplings was 36 ± 12 (1 σ) days. The concentrations at the four sampling depths in the top 100 m were averaged because they were quite variable (see Table 1) and the depth of the maximum concentration varied between sampling dates. Moreover, whereas total suspended matter and particulate aluminum consistently peaked at the same depth, particulate calcium peaked at greater depth on six of the 11 sampling dates. Concentrations below 100 m were generally lower. The basic shapes of the three curves of suspended concentrations in Fig. 2, A, C, and F, remain very similar, however, no matter whether averages over the top 100 or 200 m or the peak concentrations are plotted. We show the 0- to 100-m averages because for this depth the information density is the greatest (data for a few of the deeper samples are missing).

The deepwater flux of all components, including aluminum, during the spring peak and much of the summer of 1981 was about twice as high as in the corresponding periods of the three preceding years (*4*). This finding suggests that the near-surface production of biogenic matter was particularly high and that, along with it, the flux of abiogenic material to the deep water also increased although its proportion of the total flux decreases with increasing total-flux levels (*4*). The apparently anomalous 1981 peak emphasized the coherence between our two types of measurements, surface-water particulate concentrations and deepwater flux. The peak also presents a special problem, however, with regard to the nonbiogenic component. The earlier levels of the aluminum flux in the deep water could be accounted for in terms of the atmospheric input of clay to the surface of the Sargasso Sea (*8*); the 1981 levels are considerably higher. Our knowledge of the atmospheric input is quite limited, however, as no year-round, let alone more extended, measurements have been made. In support of the contention that the atmospheric deposition can support the deepwater flux are the particulate aluminum concentrations in the surface water, which also were higher in 1981 than those reported earlier for the Sargasso Sea (*8, 9*), although similarly high concentrations have been encountered in the Gulf Stream (*10*) and in both the North and South Atlantic (*9*). It is also possible, however, that a portion of the deepwater flux of aluminum is not of recent surface origin but is horizontally advected (*11*).

There is a similarity between the shapes of the concentration and flux curves for both the total dry mass (Fig. 2A) and calcium (Fig. 2C). The near-surface concentrations of aluminum, by contrast, appear to be random with respect to the flux at depth (Fig. 2E). This is more clearly shown in the right panels of Fig. 2, where the linearly interpolated fluxes on the dates of the suspended-matter samplings are plotted versus the suspended concentrations. The correlations are highly significant (< 1 percent probability of their being due to chance) for both total dry mass (Fig. 2B) and calcium (Fig. 2D), but no significant correlation exists for aluminum (Fig. 2F). The variability of the near-surface suspended-matter concentrations and their decrease below 100 m suggest that the concentrations reflect recent input history at or near the surface and removal below. To the extent that they do, it appears that for most of the total dry mass and for calcium both the inputs to and outputs from the surface water are related to the annual productivity cycle, but in the case of aluminum only the output shows such a relationship (Fig. 1). The aluminum input, by contrast, is related not to the same annual cycle but probably to random storm events. It is not clear at present, however, why both biogenic (as exemplified by calcium) and abiogenic (as exemplified by aluminum) particle concentrations in the surface water were unusually high in early 1981.

As was the case for our earlier data from the sediment-trap experiment (*1, 4*), the high degree of correlation between the near-surface concentrations of particles and the particle flux in deep water suggests a very rapid transfer of

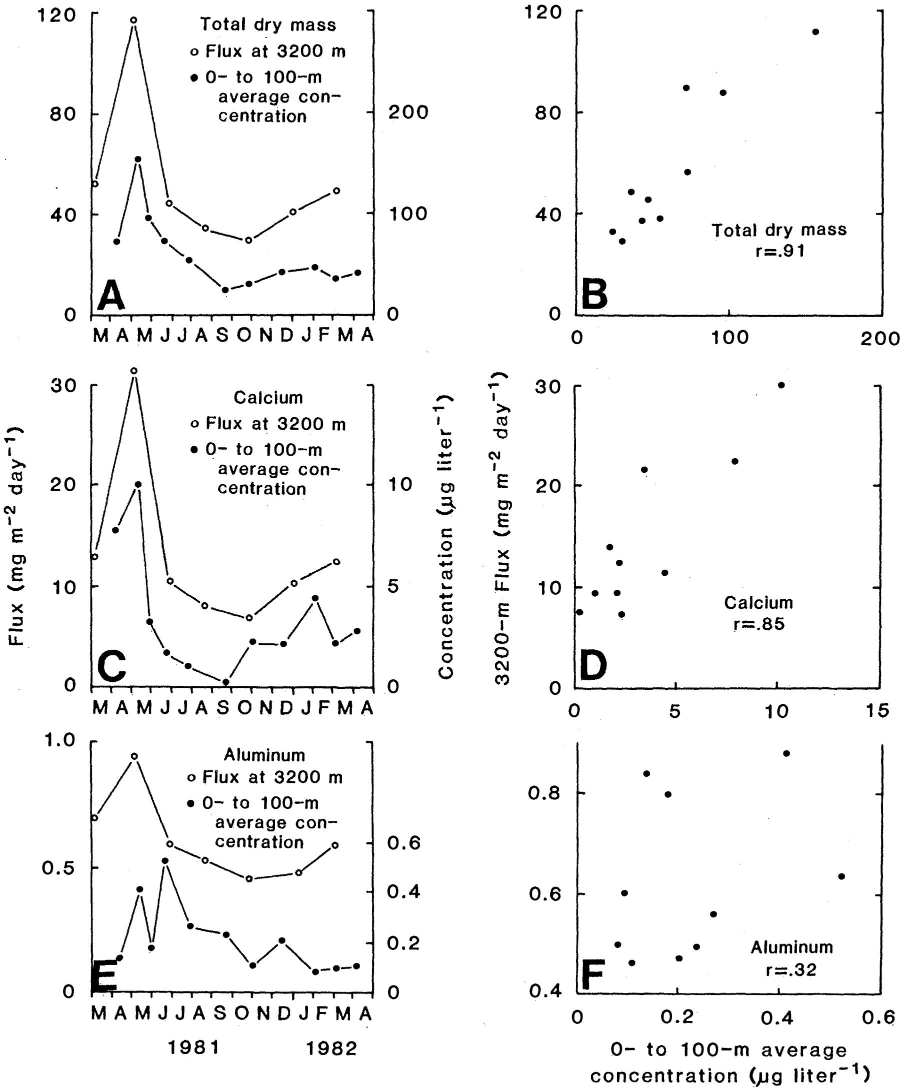

Fig. 2. Comparisons of particulate fluxes at a depth of 3200 m and average concentrations in the top 100 m of the Sargasso Sea. (A, C, and E) Graphs of variation with time; (B, D, and F) graphs of correlations. The average reproducibility of all measurements was ± 10 percent or better.

material to the deep water. The coupling is very close. Because of the inherent differences between the two types of measurements, we cannot determine sinking rates from the data; the resolving power of the sediment-trap data is 60 days. It does appear, however, that flux levels in the deepwater rise and fall in response to surface-water concentration changes on a time scale shorter than that.

By applying the concentrations shown in Fig. 2 to a 100-m water column with a cross section of 1 m^2 and dividing by the flux at depth, we determined the residence times of particulate calcium and aluminum in the top 100 m with respect to the flux at 3200 m. The values thus calculated range from 3 to 38 days for calcium and from 14 to 80 days for aluminum. Much of the calcium is concentrated in relatively rare large particles (for example, foraminiferal tests) which escape representative sampling by Niskin bottles (*12, 13*) and consequently are not included in analyses of filtered material. Therefore, the residence time of calcium is no more than a lower limit. This same sampling effect is probably also responsible for the nonzero intercept in the regression of calcium flux on calcium concentration (Fig. 2D). In the case of aluminum, we believe that the calculated residence times have significance because the input can be presumed to be in the form of small particles (clay) amenable to both bottle sampling and filtration and because the particles are resistant to biodegradation between the surface and the depth of the trap. Our values are significantly shorter than the estimate of 4 years by Krishnaswami and Sarin (*9*), which was based on an estimated standing crop of particulate aluminum in the Atlantic (determined by extrapolating surface-water concentrations over the entire water column) and the long-term deposition rate on the ocean floor. Implicit in their calculation was the assumption that the aluminosilicate particles settle individually throughout the entire water column. Our values are somewhat shorter than a hypothetical residence time of about 150 days calculated by Wallace *et al.* (*8*) for aluminum in the mixed layer of the Sargasso Sea (200 m deep). That calculation was based on aerosol and surface-water concentrations and an assigned atmospheric deposition velocity. More recently, however, Wallace *et al.* (*10*) calculated a residence time of 30 days for particulate aluminum in the top 30 m of the Gulf Stream. Although based on a quite different set of experiments and assumptions, these results and ours agree very well and lead to the same conclusion, that the small clay particles are removed from the surface water within a few weeks. In addition, our data show that thereafter the clay particles are transmitted to the deep ocean in association with organic matter at sinking rates far exceeding those of individual dust particles (*9, 10, 12*).

We do not know how such an efficient removal of clay particles is accomplished. Fecal-pellet transport is known to be an important mechanism (*14*), but it requires the existence of organisms capable of very efficiently filtering large volumes of water. Salps are likely candidates, especially where they occur in large numbers (*10, 15*). They have the ability to retain even the finest particles contained in the water they filter and to eject them in large fecal pellets. Filtration rates as high as 800 ml min^{-1} have been measured for some individuals (*16*). At this rate it would require only one individual per 100 m^3 of water to filter the entire volume in less than 90 days. Biological removal of the fine particles and production of larger ones can produce the observed patchiness in the particle concentrations. The sweeping out of the water column of the clay particles by organic aggregates other than fecal matter is another possibility but one about which few specifics are known (*17*). The latter mechanism can be effective throughout the entire water column and can affect small particles of other than surface origin (*11*).

One may speculate that, in addition to clay particles, other finely distributed abiogenic debris is similarly removed from the surface ocean and transmitted to deep water. Since the packaging of such fine debris into larger particles held together by mucus or organic membranes requires the expenditure of energy by the packagers, there might be an evolutionary or ecological advantage in that activity. One likely advantage ac-

Table 1. Concentrations of total particulate matter, particulate calcium, and particulate aluminum in the upper 200 m of the Sargasso Sea.

Depth (m)	Sampling date										
	9 April 1981	11 May 1981	28 May 1981	19 June 1981	28 July 1981	18 September 1981	30 October 1981	15 December 1981	5 February 1982	4 March 1982	2 April 1982
					Total particulate matter (μg $liter^{-1}$)						
10	49	180	129	86	45	37	38	61	61	44	60
25	83	116	72	78	105	19	30	68	46	44	37
50	132	308	131	77	43	28	32	19	48	34	36
100	24	20	52	52	28	18	21	25	32	24	26
150	26		28	39	36	15	12	15	20	15	13
200			55	51	53	10	10		16	8	12
					Particulate calcium (μg $liter^{-1}$)						
10	2.3	11.2	5.4	0.9	0.3	0.3	2.2	2.6	5.4	2.4	3.1
25	3.1	9.1	3.3	1.4	2.4	0.2	1.5	0.8	4.4	2.5	2.5
50	23.5	3.3	3.1	0.5	0.8	0.2	2.1	1.3	4.3	2.6	2.6
100	2.5	16.8	1.5	4.2	0.5	0.1	3.3	3.7		1.2	3.1
150	2.4		2.4	2.4	2.2	0.7	1.2	1.6	3.1	1.7	2.2
200	0.6		3.0	2.1	2.4	0.2	1.1		2.8	1.4	1.5
					Particulate aluminum (ng $liter^{-1}$)						
10	161	335	286	989	311	480	142	183	115	97	144
25	115	265	213	877	501	192	126	437	102	127	97
50	188	817	172	166	180	103	93	65	47	47	94
100	79	212	35	57	88	173	62	122		92	84
150	77		50	88	65	75	69	71	60	61	46
200	21		114	152	64	181	98		60	64	97

cruing from it to the organisms is the rapid removal of indigestible matter from their feeding environment. The rapid sinking out of all useless particulate matter eliminates the need to reprocess it repeatedly, an activity that costs energy but yields none. The packaging of useless matter into larger particles may represent a net saving. It appears that, without this activity of the organisms, the fine-particle concentrations in the surface waters of the ocean would build up to much higher levels.

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6 August 1982

Lizard Tail Autotomy: Function and Energetics of Postautotomy Tail Movement in *Scincella lateralis*

Abstract. *Handling of autotomized, thrashing and autotomized, exhausted tails of the lizard* Scincella lateralis *by mammals and snakes was tested to examine the function of postautotomy tail movement. Tail movement attracted a mammal's attack to the tail, permitting the lizard to escape and increased the time required for a snake to subdue a tail before swallowing it, increasing the lizard's escape time by 40 percent. Lactate concentrations of autotomized tails after movement were compared to those of intact tails after rest in* S. lateralis, *a species with a high rate of autotomized tail thrashing, and* Anolis carolinensis, *a species with a low rate of thrashing. Postautotomy movement increased tail lactate concentration in both species, but mean tail lactate concentration in* S. lateralis *was 60 percent higher than that in* A. carolinensis, *and a third higher than that reported for whole-body lactate content of the very mobile lizard* Dipsosaurus dorsalis.

Autotomy of body parts has evolved independently in vertebrates (*1, 2*) and invertebrates (*3*) as a predator defense in which mechanical release of the structure facilitates escape (*4*). In general, an autotomous structure is relatively simple in morphology with few interacting variables and has an alternative biological role, such as locomotion or feeding. Thus, autotomy offers a simplified model system for studying several important topics of evolutionary biology—for example, the costs of predator defense mechanisms, apportionment of resources to somatic versus reproductive components, and the evolution of predator-prey interactions (*5, 6*). A postautotomy phenomenon characterized by an extended period of muscle contraction in the autotomized structure occurs in several groups: decapods, arachnids (*7*), salamanders (*1*), and lizards (*8*) are examples. The tail in some species of lizards may thrash rapidly from side to side immediately after autotomy (*8*). Although postautotomy tail movement has been of interest for nearly a century (*9*), neither the function nor energetics involved is clear (*10–12*). We report experimental evidence indicating that postautotomy tail movement either distracts predators from escaping lizards or increases handling time of the released tail, allowing more time for prey escape (or both), and that such tail movement is supported by anaerobic metabolism, the capacity of which is greater in species that use autotomy as a principal predator escape tactic.

Lizards constitute an important dietary component of mammals (*13, 14*) and snakes (*15*). Because the feeding mechanics and behavior of these predators differ considerably (*14, 16*), the effects of autotomized tail movement on predator handling might vary among predator types. Because capturing prey for many mammal species involves manipulation with forelimbs before ingestion, prey are periodically free from a mammal's grip, and a mammal's attention is focused on the most active part of the prey (*14*). We thus hypothesized that movement of an autotomized tail should function to attract and maintain a mammal's attention on a tail and away from an escaping lizard. In contrast, a prey item is rarely free from a snake's grip. In addition, many snake species, in particular those that subdue prey by constriction, do not manipulate prey before prey movement has subsided (*16*). We hypothesized that autotomized tail movement should increase the time required for a snake to handle a tail, thereby allowing more time for prey escape.

To examine whether postautotomy tail movement distracts predators, we staged encounters between lizards of two species and a feral cat (*Felis catus*, 5.5 kg). We chose the lizards *Scincella lateralis* and *Anolis carolinensis* (*17*) because of their high and low rates of tail thrashing (*18*). Tail autotomy is the principal escape tactic of *S. lateralis*, which relies on autotomy to a greater extent than does *A. carolinensis* (*18*); *A. carolinensis* uses several alternative escape tactics. We recorded the cat's reaction to lizards of both species plus their autotomized and thrashing tails and their autotomized and exhausted tails (*19*). To examine whether postautotomy tail movement increases predator handling time, we staged encounters between *S. lateralis* and a snake, *Lampropeltis triangulum*, again using both autotomized and thrashing tails and autotomized and exhausted tails (*20*). For each tail, we measured total handling time and two of its components: subdue and ingestion time (*21*). To examine whether postautotomy tail movement is supported by anaerobic metabolism and is greater in species that chiefly use autotomy, we compared lactate concentrations of autotomized tails after thrash-