minor and trace elements from seawater and incorporate these elements in their skeletons. Electron microprobe analyses of phosphorus in the calcite skeletons of calcareous nannoplankton show that, after a middle Eocene high, these plants incorporated low, but fluctuating amounts of phosphorus from early Oligocene to middle Miocene times (*16*). A slight, but steadily increasing phosphorus uptake occurs from late Miocene times onward (*16*). I believe that this increase reflects greater availability of phosphorus in the water from late Miocene times, since phosphorus is one of the major nutrients supplied by upwelled waters.

Sedimentological, paleontological, and geochemical evidence indicate that the Benguela upwelling system off northern Namibia originated in the early late Miocene (about 10 million years before the present). The evidence presented actually establishes the times of initiation of upwelling above site 362/362A only. Whether upwelling began all along the western coast of southern Africa at the same time is a moot point. Intuitively, it seems that, once the atmospheric and other conditions that drive the Benguela upwelling were in effect, upwelling would begin all along the coast with only a slight delay from place to place.

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Sediment-Water Chemical Exchange in the Coastal Zone Traced by in situ Radon-222 Flux Measurements

Abstract. *In situ radon-222 flux experiments conducted in benthic chambers in Cape Lookout Bight, a small marine basin on the North Carolina coast, reveal that enhanced chemical transport across the sediment-water interface during summer months is caused by abiogenic bubble tube structures. Transport rates for dissolved radon, methane, and ammonium more than three times greater than those predicted on the basis of molecular diffusion occur when open tubes are maintained by semidiurnal low-tide bubbling.*

Chemical exchange across the sediment-water interface is an important process regulating the composition of the oceans (*1*). In the coastal zone, organic-rich sediments can supply a major fraction of the nutrient requirements of primary producers in overlying water (*2*). The sediments are the site of intense remineralization during which microbial heterotrophs convert deposited organic carbon, nitrogen, and other elements into dissolved NH_4^+, HCO_3^-, CH_4, and other chemical species (*3*). The remineralization reactions together with diffusive transport, adsorption, and other processes produce concentrations of these products in the interstitial waters of the sediments which generally increase with depth. The rates of transport of the dissolved species from the sediments to the water column are, in turn, controlled by both the magnitude of the resulting concentration gradients in the interstitial water and the mechanism of sediment-water exchange.

Transport by molecular diffusion can be predicted by Fick's first law, modified for application to sediments (*4*):

$$J = -\phi D_s(\partial C/\partial z)_{z=0} \qquad (1)$$

where J is the vertical diffusive flux across the sediment-water interface, ϕ is the sediment porosity, D_s is the whole (bulk) sediment diffusion coefficient (*4*), and $(\partial C/\partial z)_{z=0}$ is the vertical concentration gradient in the interstitial water at the interface.

One calculates fluxes across the sediment-water interface in the ocean by means of Eq. 1, using measured porosities and concentration gradients coupled with estimated molecular diffusion coefficients, since molecular diffusion coefficients are difficult to measure experimentally. However, if the flux as well as the porosity and concentration gradient

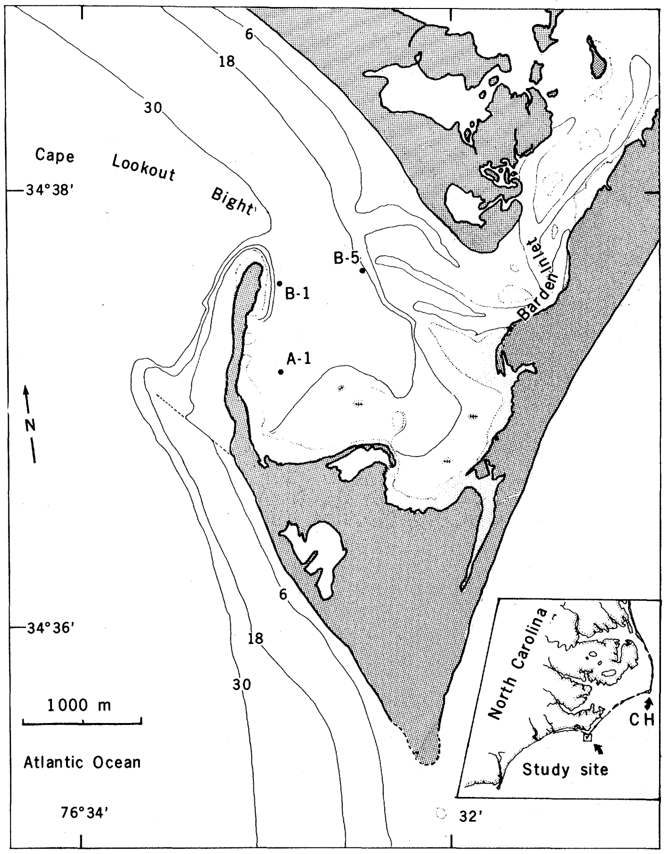

Fig. 1. The Cape Lookout Bight, North Carolina, study site located approximately 110 km southwest of Cape Hatteras (*CH*). Flux studies were conducted at station A-1. Currents at station A-1 are generally < 6 cm sec^{-1} near the bottom and as high as 28 cm sec^{-1} near stations B-1 and B-5 during ebb and flood tide. Depth contours are in feet.

for the species of interest are measured, Eq. 1 can be rearranged so that one calculates an experimentally defined or "apparent" whole sediment diffusion coefficient, termed D_s'. If the D_s' values obtained exceed the theoretical molecular sediment diffusivities, some process that enhances the sediment-water exchange is implicated.

Recent field studies of the exchange of CH_4 (5) and NH_4^+ (6) between the sediment and water in Cape Lookout Bight, North Carolina (Fig. 1), have yielded summertime chemical fluxes (Fig. 2) more than three times greater than those predicted on the basis of molecular diffusion as calculated from Eq. 1. The CH_4 D_s' values calculated as described above are also enhanced up to threefold. Macroinfaunal irrigation and physical sediment mixing often invoked to explain such enhanced transport from nearshore sediments (7-9) are not important in the bight during summer months (5); however, two alternative hypotheses can be generated to explain these results.

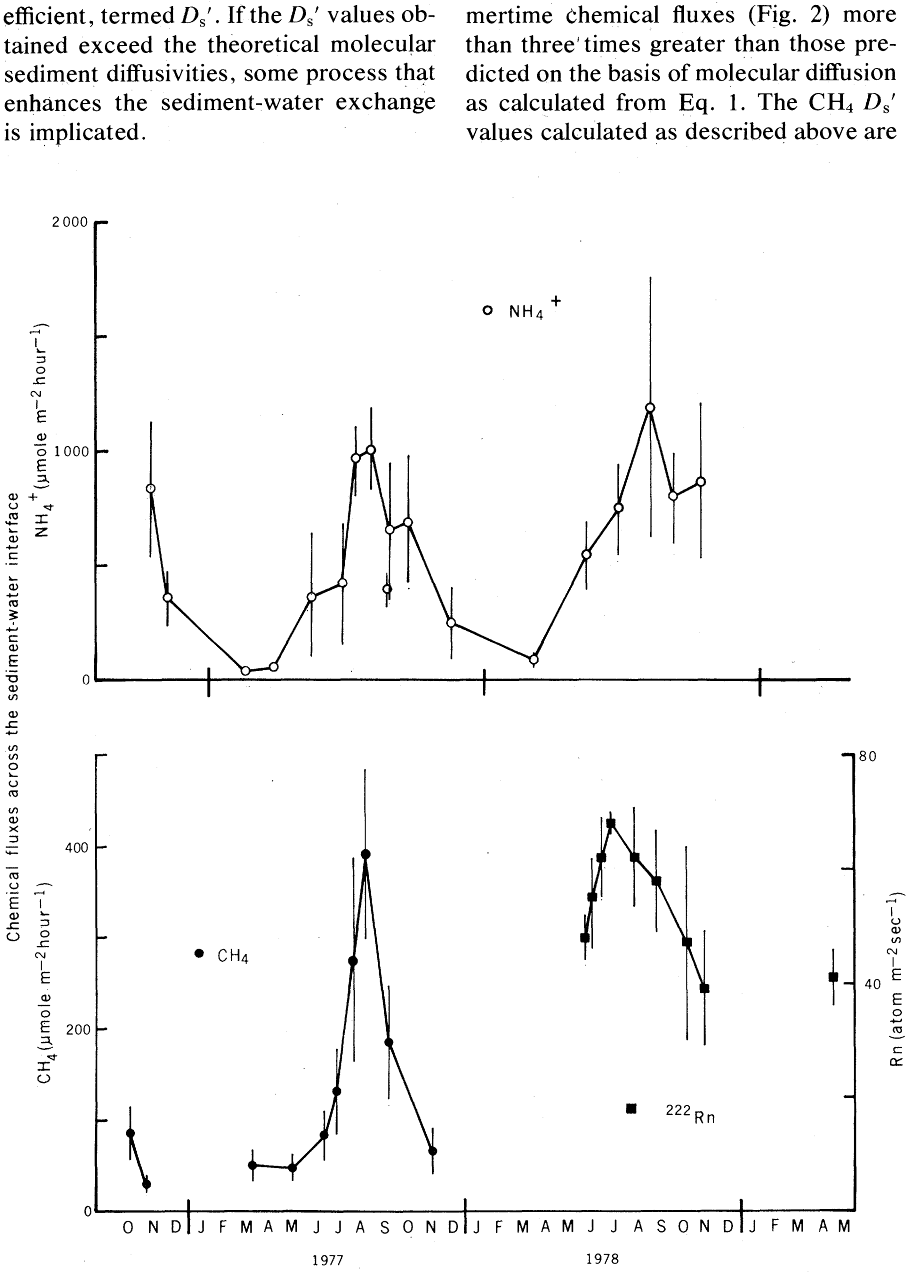

Fig. 2. Seasonal variations in chemical fluxes across the sediment-water interface observed in Cape Lookout Bight, North Carolina. In situ benthic chambers were used. Error bars (1σ, where σ is the theoretical standard deviation) are calculated from multiple chamber emplacements.

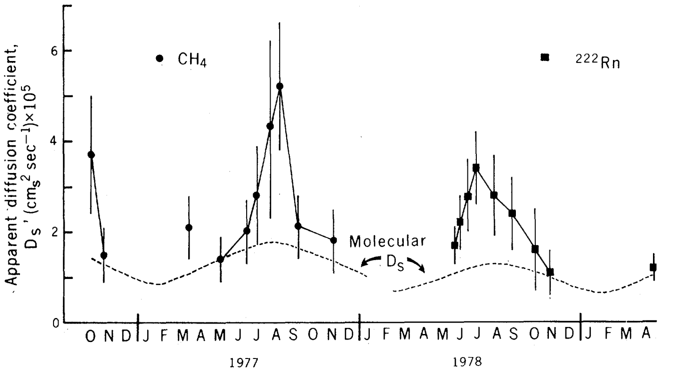

Fig. 3. Seasonal variations in the apparent sediment diffusivities (D_s') calculated from in situ CH_4 and ^{222}Rn flux measurements in benthic chambers in Cape Lookout Bight. Theoretical molecular sediment diffusivities (D_s) for CH_4 and ^{222}Rn are also shown. Error bars = ± 1σ.

The first hypothesis postulates open tubes in bight sediments maintained by low-tide bubble ebullition during summer months (5, 8). The bubbling results from rapid CH_4 production and the attainment of saturation concentrations within 10 cm of the sediment-water interface (5). The cylindrical bubble tubes, which penetrate in the sediments to depths of greater than 5 cm, commonly range from 2 mm to 2 cm in diameter. We hypothesize that they enhance transport through the creation of additional exposed surface area and increased concentration gradients between overlying water trapped in tubes and deeper interstitial water enriched in dissolved CH_4 and NH_4^+.

According to the second hypothesis, enhanced fluxes result from significant CH_4 and NH_4^+ production in organic-rich flocculent material resting at the sediment-water interface. Verification of either hypothesis has important consequences for understanding biogeochemical cycling in the coastal zone and other organic-rich environments.

We report here the results of direct in situ ^{222}Rn flux measurements which can be used to test these hypotheses. This radioactive noble gas, unlike CH_4 and NH_4^+, is not subject to microbial and chemical transformations. A radon flux at our site above that predicted on the basis of molecular diffusion would support the bubble tube hypothesis. These are among the first in situ radon transport studies conducted with benthic chambers, and they demonstrate the feasibility of the technique (10).

The theoretical and analytical basis for the use of radon as a tracer in sediments has been established by Broecker (11) and was recently discussed by Hammond and his co-workers (9, 10). The distribution of radon in sediments is controlled by a balance between production from its parent isotope, ^{226}Ra, diffusion and other transport processes, and radioactive decay (half-life, 3.83 days). The radon flux across the sediment-water interface may be calculated from Eq. 2 (11, 12):

$$J = (D_s\lambda)^{1/2}(C_{eq} - C_0) \qquad (2)$$

where C_{eq} is the radon concentration [atoms or disintegrations per minute (dpm) per cubic centimeter of wet sediment] in equilibrium with sedimentary ^{226}Ra, C_0 is the radon concentration at the sediment-water interface (assumed to be equal to the value for the overlying water), and $\lambda = 2.1 \times 10^{-6}$ sec^{-1}. Measurements of J, C_{eq}, and C_0 allow for direct calculation of D_s' values. A similar result for CH_4 and ^{222}Rn in the bight would imply a common mechanism for the elevated sediment-water exchange observed during the summer.

Table 1. In situ ^{222}Rn sediment-water flux measurements and calculated apparent sediment diffusivities (D_s'). Errors = ± 1σ.

Date (1978)	Sediment temperature (°C)	Benthic chamber	Time (hours)	Radon flux (atom m^{-2} sec^{-1})*		$D_s' \times 10^5$ (cm_s^2 sec^{-1})
				Individual	Mean	
White Oak River estuary						
20–21 July	25.2	A	21.5	133 ± 17	135 ± 2	1.2 ± 0.2†
20–21 July	25.2	X	21.5	136 ± 17		
Cape Lookout Bight						
6–7 June		B	21.0	48 ± 4	48 ± 4	1.7 ± 0.4
15–16 June	22.1	B	22.3	63 ± 5	55 ± 7	2.2 ± 0.6
15–16 June	22.1	C	22.3	51 ± 5		
15–16 June	22.1	X	22.3	52 ± 5		
27–28 June	23.4	B	19.5	62 ± 7	62 ± 7	2.8 ± 0.8
11–12 July	24.5	B	18.3	69 ± 6	68 ± 2	3.4 ± 0.8
11–12 July	24.5	C	18.1	67 ± 6		
10–11 August	27.5	A	21.7	55 ± 5	62 ± 9	2.8 ± 0.9
10–11 August	27.5	X	19.2	68 ± 6		
10–11 August	27.5	X (nb)‡	5.5	62 ± 9		
8–9 September	26.8	B	21.4	64 ± 5	58 ± 9§	2.4 ± 0.8
8–9 September	26.8	C	19.4	51 ± 5		
8–9 September	26.8	X§	21.2	> 52		
8–9 September	26.8	X (nb)‡	4.8	42 ± 8		
16–18 October	21.4	X (b)‡	3.5	47 ± 17	47 ± 17	1.6 ± 0.9
10–11 November	19.0	B	22.0	37 ± 3	39 ± 10	1.1 ± 0.5
10–11 November	19.0	C	22.8	50 ± 4		
10–11 November	19.0	X	21.3	30 ± 4		
30 April 1979	20.0	B	23.5	41 ± 5	41 ± 5	1.2 ± 0.3

*The radon flux in dpm per square meter per minute can be recalculated through multiplication by both λ (1.259×10^{-4} min^{-1}) and 60 sec min^{-1}. †Calculated from $C_{eq} = 2703 \pm 301$ atom cm_s^{-3} (0.34 ± 0.04 dpm cm_s^{-3}). ‡Short-term experiments during nonbubbling (nb) and bubbling (b) periods. §The mean was calculated from the data of chambers B and C only; chamber X was inadvertently diluted with an unknown volume of seawater at the conclusion of the experiment.

We measured radon fluxes in situ by monitoring concentration changes in diver-emplaced benthic chambers with known water volume and sediment surface area coverage (*5*, *6*). Two or three 10- to 20-liter radon sample bottles (*13*) and a battery-operated submersible bilge pump were attached in series to each chamber. Water trapped in the system was mixed for 60 to 90 minutes before the initial samples were taken and before subsequent intermediate or final samples were taken (*14*). The technique was tested in the nearby White Oak River estuary at an upriver station where we expected molecular diffusion to dominate (*15*). Results from this test yielded reproducible fluxes and a mean calculated D_s' value of 1.2×10^{-5} cm^2 sec^{-1} (Table 1), which is in reasonable agreement with theoretical molecular diffusion values (*4*) tabulated by Broecker and Peng (*16*).

Experiments in Cape Lookout Bight were conducted for 3- to 23-hour periods. We used increases in the radon concentrations in the chambers to calculate radon fluxes, using the equation:

$$J = \frac{V\lambda[C_f - C_0 \exp(-\lambda t)]}{A[1 - \exp(-\lambda t)]} \quad (3)$$

where V is the total volume of the chamber plus the sample bottles, A is the surface area of sediment trapped by the chamber, and t is the time between taking the initial (C_0) and intermediate or final (C_f) radon bottle samples. We also measured CH_4 and NH_4^+ fluxes between low-tide bubbling episodes during the radon experiments, using 60-ml syringe samples taken directly from the chambers during the first few hours of each experiment. The results of the radon flux measurements (Table 1) obtained during June through November 1978 and in April 1979 in Cape Lookout Bight are plotted in Fig. 2.

A mean C_{eq} value of 810 ± 131 atoms per cubic centimeter of wet sediment (0.102 ± 0.017 dpm cm^{-3}) was obtained from eight sediment cores at our site. Variations in C_{eq} in sediment sections 2 to 5 cm thick in the upper 20 cm do not exceed the analytical error.

Radon D_s' values calculated by the use of Eq. 2 and above data are plotted in Fig. 3 along with 1976–1977 CH_4 results. The similarity of D_s' values for both species supports the bubble tube hypothesis since elevated transport of radon cannot be attributed to chemical or microbial processes. It is conceivable that radon transport could be elevated directly by low-tide bubbling during the longer experiments (18 to 23 hours) (CH_4 and NH_4^+ flux experiments were conducted over 1 to 4 hours during nonbubbling high-tide intervals). No significant differences were seen in 3- to 5-hour radon experiments carried out between periods of low-tide bubbling and during active bubbling (Table 1); however, larger experimental errors and fewer data precluded conclusive results.

Preliminary studies of vertical interstitial-water radon distributions (*17*) in sediments away from bubble tubes yield D_s values in agreement with predictions of molecular diffusion. These results further suggest that bubble tubes play a role in sediment-water exchange.

We conclude that the enhanced transport observed in Cape Lookout Bight for CH_4 and nutrient elements is associated with the abiogenic bubble tube structures. Enhanced sediment-water chemical exchange can therefore occur in organic-rich coastal sediments in the absence of macroinfaunal irrigation and current-induced physical mixing. Radon-222 is an excellent in situ tracer for such processes in the coastal zone.

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12. The general equation describing the radon distribution in sediments is (*11*)

$$\frac{dC}{dt} = D_s \frac{\partial^2 C}{\partial z^2} + \lambda C_{eq} - \lambda C \qquad (4)$$

where C is the measured radon concentration in atoms per cubic centimeter or disintegrations per minute per cubic centimeter of bulk sediment. The steady-state solution to Eq. 4 is

$$C = C_{eq}\{1 - \exp[-(\lambda/D_s)^{1/2}z]\} + C_0 \exp[-(\lambda/D_s)^{1/2}z] \qquad (5)$$

In the bight water column, C_0 is approximately 0.5 to 2 dpm liter^{-1}. The radon flux across the sediment water interface is given by

$$J = -D_s(\partial C/\partial z)_{z=0} = -(\lambda D_s)^{1/2}(C_{eq} - C_0) \qquad (6)$$

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14. We conducted a series of mixing experiments, using a benthic chamber system in an artificial pond. Two or three samples were taken simultaneously at set time intervals for radon analysis; 99 percent mixing was obtained in 60 minutes, and the results agreed with numerical solutions to a set of mixing equations for the system.
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18. We thank G. Miller, J. Chanton, S. Marocchi-Klump, F. Sansone, P. Crill, and K. Gruebel for assistance with field and analytical work. We are grateful to G. Mathieu and other personnel of Lamont-Doherty Geological Observatory for assistance with radon equipment design and fabrication and ^{226}Ra standards. We thank the University of North Carolina, Institute of Marine Sciences, Morehead City, for use of boats and laboratory space. Financial support was provided by grants OCE75-06199 and OCE78-9453 from the Marine Chemistry Program, Oceanography Section, National Science Foundation.

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Seizure Protection and Increased Nerve-Terminal GABA: Delayed Effects of GABA Transaminase Inhibition

Abstract. *Changes in γ-aminobutyric acid (GABA) occurring in the presence and in the absence of GABA-containing nerve terminals were estimated in rats in which the dense GABA projection to the substantia nigra was surgically destroyed on one side of the brain. The net increase in GABA of the denervated nigra was compared with that of the intact nigra at various times after a single injection of γ-vinyl-GABA, which irreversibly inhibits GABA transaminase. Total GABA reached a maximum within 12 hours, but the GABA pool associated with nerve terminals did not increase until 36 hours and peaked at 60 hours. The onset and peak of anticonvulsant activity against maximal electroshock seizures directly paralleled the time course for the increase in GABA in nerve terminals, but was not positively correlated with that independent of the terminals. This result supports the concept that elevating GABA in nerve terminals facilitates GABA-mediated synaptic transmission and predicts anticonvulsant activity.*

The recent availability of compounds that selectively alter either the concentration of γ-aminobutyric acid (GABA) or the activity of neuronal GABA receptors has provoked a resurgence of investigations into the neurotransmitter role of this amino acid (*1*). A major obstacle encountered in these studies is that of discriminating between the GABA compartment associated with nerve terminals and other compartments of GABA. Throughout the brain, synthesis, uptake, and degradation of GABA take place both in GABA-containing nerve terminals and in cells (glial and neural) that do not use this compound as a neurotransmitter (*2, 3*). As a result, the degree to which changes in endogenous GABA can be expected to influence GABA-mediated synaptic transmission is difficult to ascertain (*3*).

The relationship between elevation of brain GABA and protection against electrically or chemically induced seizures in animals illustrates this problem. Drugs that decrease brain GABA or block GABA receptors can induce seizures in a variety of species (*4*), whereas drugs that enhance GABA transmission have anticonvulsant properties (*5*). However, quantitative changes in the amount of brain GABA are often poorly correlated with susceptibility to seizures (*6*). Ideally, one would like to be able to predict the degree of seizure protection to be expected from a given elevation in brain GABA. The achievement of this goal is complicated by our inability to determine what portion of the increased GABA concentration is available for release at synaptic terminals (*3*).

The importance of this issue is underscored by the apparently discordant biochemical and pharmacological actions of γ-vinyl-GABA, a specific and irreversible inhibitor of GABA transaminase (*7*). This compound has been reported to be relatively ineffective as an anticonvulsant agent in several animal seizure tests, despite its ability to increase GABA in whole brain and in various brain regions (*8*). We hypothesized that some major portion of the GABA increase produced by this agent might be sequestered in compartments that do not directly participate in GABA-mediated synaptic transmission. We obtained evidence in support of this hypothesis by experimentally discriminating between nerve-terminal–dependent and nerve-terminal–independent changes in GABA (*9*). We also discovered, however, that γ-vinyl-GABA possesses marked anticonvulsant activity which became evident only after a 2-day latency. To our knowledge, these experiments provide the first documentation that γ-vinyl-GABA can protect rats against tonic seizures produced by maximal electroshock and show that the appearance of this action coincides with an increase in nerve-terminal–dependent GABA.

We assessed the effect of γ-vinyl-GABA on the duration of the tonic hindlimb extension component of maximal electroshock seizures. Duration of tonic hindlimb extension was unchanged 12 hours after γ-vinyl-GABA was administered (600 to 1600 mg per kilogram of body weight, injected intraperitoneally). However, 36 hours after the injection (1600 mg/kg) the duration of tonic hindlimb extension was significantly attenuated, and by 60 hours complete suppression was observed. Since antiseizure activity was maximal at 60 hours (Fig. 1), the dose-dependency of the effect was examined at this time (Fig. 2). The mean effective dose (ED_{50}) was about 900 mg/kg; the dose-effect function parallels that obtained with sodium valproate [*n*-dipropyl acetate (DPA)], a drug used to treat human epilepsy.

To examine the possibility that γ-vi-