

Bacterial scavenging of ^{234}Th in surface ocean waters

T. Lee¹, E. Barg¹, D. Lal¹, F. Azam²

¹Scripps Institution of Oceanography, Geological Research Division, La Jolla, California 92093-0220, USA

²Scripps Institution of Oceanography, Marine Biology Research Division, La Jolla, California 92093-0202, USA

ABSTRACT: ^{234}Th was determined in the dissolved ($<0.1\ \mu\text{m}$), bacterial (0.1 to $1.0\ \mu\text{m}$) and 2 larger particulate pools (1 to $5\ \mu\text{m}$ and $>5\ \mu\text{m}$) at 5 or 6 depths in the upper 120 m of the water column at a station ($31^\circ 51.6'$ N, $119^\circ 31.9'$ W) in the Southern California Bight during October 1989 and July 1990. Depth profiles of bacterial abundance and chlorophyll *a* were also measured. The bacterial fraction had high volume concentration factor (VCF: 1 to 4×10^6) and the highest estimated $^{234}\text{Th}/\text{C}$ ratio of all size fractions (5.1 and $5.5\ \text{nCi gC}^{-1}$). The VCF for ^{234}Th scavenging by bacteria determined in a microcosm experiment (containing a $2\ \mu\text{m}$ filtrate of seawater from Scripps pier and spiked with ^{234}Th) was on the order of 7×10^6 . Both the bacteria fraction and $>5\ \mu\text{m}$ fraction had $^{234}\text{Th}/\text{C}$ ratios comparable to that computed for the colloidal fraction. Sequential transfer of ^{234}Th (truly dissolved ^{234}Th \rightarrow disperse colloids \rightarrow suspended particles \rightarrow sinking particles) alone does not explain the observed high $^{234}\text{Th}/\text{C}$ ratio in the bacterial and the large particulate fractions. We propose that the abundant and highly ^{234}Th -reactive colloids (which occur bound to the surfaces of free and particle-bound bacteria in addition to their occurrence in the disperse phase) contribute substantially to efficient scavenging of ^{234}Th by bacteria as well as colonized particles of all sizes. The contribution by bound colloids may vary with the physiological states of bacteria and phytoplankton and their state of aggregation. This unstructured flow model has implications for models which use $^{234}\text{Th}/^{238}\text{U}$ disequilibrium as an indicator for downward flux of particles in the ocean.

INTRODUCTION

The particle-reactive ^{234}Th (half-life = 24.1 d) is often in disequilibrium with its parent nuclide ^{238}U in surface ocean waters. The disequilibrium occurs because ^{234}Th but not ^{238}U becomes associated with sinking particles. Consequently, $^{234}\text{Th}/^{238}\text{U}$ disequilibrium is potentially a powerful tool in the study of the downward flux of carbon in the ocean via sinking particles (Bhat et al. 1969, Coale & Bruland 1985, Murray et al. 1989).

The interpretation of $^{234}\text{Th}/^{238}\text{U}$ disequilibrium in terms of carbon fluxes requires a knowledge of the mechanisms and pathways leading up to the association of ^{234}Th to sinking particles as well as of the $^{234}\text{Th}/\text{C}$ ratios of the sinking particles. Several models have been proposed to explain ^{234}Th association with sinking particles. The simplest of these models (Bhat et al. 1969) assumed direct adsorption of dissolved ^{234}Th onto sinking particles and led to an average settling

velocity of $\text{ca } 2 \times 10^{-3}\ \text{cm s}^{-1}$ for these particles. Subsequently, observational data on thorium isotopes ^{234}Th and ^{230}Th in the surface and deeper layers of the ocean necessitated more complex scavenging models (Bacon & Anderson 1982, Huh & Beasley 1987, Nozaki et al. 1987, Taguchi et al. 1989). These models suggest active partitioning of thorium isotopes between particulate (fine and large suspended particles) and dissolved phases. In surface waters, the observed large $^{234}\text{Th}/^{238}\text{U}$ disequilibria (Bhat et al. 1969, Coale & Bruland 1985, Huh & Beasley 1987, Murray et al. 1989) clearly show the primary removal of dissolved ^{234}Th by fast-settling particulates. However, from basic considerations, it would be expected that ^{234}Th would be scavenged primarily by colloids and fine suspended particles, because of their larger surface to volume ratios. The observed rapid removal of ^{234}Th from the surface waters, within 3 to 4 wk, would then suggest that fine particles are quickly scavenged by larger particles.

A more recent view is that the dominant initial step is the adsorption of ^{234}Th onto colloids (Niven & Moore 1988, Baskaran & Santschi 1992, Baskaran et al. 1992) present in seawater and that the colloids are in turn scavenged by suspended particles which are scavenged by the sinking particles (Honeyman & Santschi 1989). The 'colloidal pumping' model of Honeyman & Santschi (1989) is attractive because recent work has shown that an appreciable fraction of dissolved organic carbon (DOC) exists as colloids (cf. Moran & Moore 1989, Benner et al. 1992). It has also been shown that colloids in seawater are rich in polysaccharides (Benner et al. 1992) which is relevant because polysaccharides have high affinity for ^{234}Th (Nash & Chopin 1980).

Cho & Azam (1988) proposed that pelagic bacteria, because of their large surface to volume ratio, may be major scavengers of ^{234}Th , and postulated that the scavenging of bacteria by rapidly sinking particles may be a major mechanism for the downward flux of ^{234}Th . These authors and Fuhrman et al. (1989) found that bacterial carbon was often the dominant pool of the particulate organic carbon (POC). In the water columns of Santa Monica Basin, off California, USA, and the central north Pacific gyre bacterial carbon ranged from 30 to 70% of the total POC. In addition to bacteria, the 0.1 to 1.0 μm fraction has recently been shown to also contain 'sub-micrometer particles' (0.3 to 0.7 μm : 10^{10} l^{-1} ; Koike et al. 1990). Baskaran et al. (1992) found that 0.45 μm filtrable material retained by 10 000 Da molecular sieves was accompanied by the retention of 15 to 70% of ^{234}Th .

In this study we measured ^{234}Th in the 'dissolved' (passing 0.1 μm filter) fraction and in 3 'particulate' size fractions: 0.1 to 1.0 ('bacterial'), 1.0 to 5.0 and > 5.0 μm . We also estimated ^{234}Th 'uptake' by natural assemblages of bacteria in seawater by spiking a 2.0 μm filtrate (which should contain free bacteria and some contaminating protozoa) with ^{234}Th . The purpose of this experiment was to estimate bacterial 'uptake' of ^{234}Th (per cell and per g C) to help understand the significance of bacteria in ^{234}Th uptake in field samples.

MATERIALS AND METHODS

Field measurements for ^{234}Th in seawater samples were performed in Southern California Bight during October 1989 and July 1990 at CALCOFI (California Cooperative Oceanic Fisheries Investigations) Stn #93.60 (31° 51.6' N, 119° 31.9' W). ^{234}Th was measured in various size fractions in the field samples as follows:

(1) ^{234}Th filtrable through 1 μm filter was measured in 200 l seawater from each sampling depth by pumping seawater through 1 μm polypropylene filters (Hytrex®). ^{234}Th was determined following $\text{Fe}(\text{OH})_3$ precipitation (Bhat et al. 1969, Coale & Bruland 1985).

The chemical efficiency of Th extraction was determined by spiking the seawater samples with ^{228}Th carrier (in equilibrium with ^{232}U) prior to $\text{Fe}(\text{OH})_3$ precipitation. The efficiency of Th extraction was based on the yield of ^{228}Th ; its activity was determined using an α -counter (Canberra®).

(2) Particulate ^{234}Th in different size fractions, > 5 μm , > 1 μm and > 0.1 μm , was determined by sequential filtration; 5 to 20 m^3 seawater from 5 to 6 depths from surface to 120 m were filtered sequentially through 5 μm and 1 μm polypropylene cartridge-type filters (Hytrex®) and a 0.1 μm (MTS® or Asypore®) filter on board ship using a positive displacement pump. (We recognize that size fractions as operationally defined here may not be precise because of the possibility of some trapping of particles smaller than the rated pore size of the filter.) After filtration, the filter cartridges were rinsed with deionized water, dried and ashed. The ash was counted for ^{234}Th gamma activity (63.3 keV) on a 100 cc well-type intrinsic high purity Ge crystal photon detector (ORTEC®) in J-configuration (Lee et al. 1991). The background counting rate in the photopeak was 0.56 cpm. The ^{234}Th content in various fractions was determined from the raw data by subtraction: ^{234}Th in < 0.1 μm fraction = (^{234}Th in 1 μm filtrate) - (^{234}Th in 0.1 to 1 μm fractions); ^{234}Th in 0.1 to 1 μm fraction = ^{234}Th passing 1 μm filter cartridge but retained by the 0.1 μm filter cartridge; ^{234}Th in 1 to 5 μm fraction = ^{234}Th passing 5 μm filter cartridge but retained by 1 μm cartridge; ^{234}Th in > 5 μm fraction was that retained on 5 μm filter cartridge.

Bacterial abundance was determined by epifluorescence microscopy of 4',6-diamidino-2-phenylindole (DAPI) stained samples (Porter & Feig 1980). Samples were fixed with borate buffered formalin (4% final concentration). Salinity was measured using a conductive salinometer. Chlorophyll (chl *a*) was measured using a fluorometric technique (Yentsch & Menzel 1963, Holm-Hansen et al. 1965).

In order to measure uptake of spiked ^{234}Th by bacteria (probably via adsorption on cell surface; Fisher et al. 1987) we used seawater which had been filtered through 2 μm filter to remove most organisms larger than bacteria. We realized that some protozoa and most cyanobacteria of the genus *Synechococcus* would pass through the 2 μm filter. *Synechococcus* are Gram-negative photoautotrophic bacteria which, because they fix carbon rather than remineralize it, are generally not considered along with the heterotrophic bacteria in studies of the biogeochemical roles of bacteria. This physiological distinction between *Synechococcus* and other bacteria, while fundamental in studies of carbon fluxes, may not be relevant in understanding the role of bacteria in ^{234}Th adsorption. Indeed, it has been shown that *Synechococcus* has high affinity for ^{234}Th

(Fisher et al. 1987). Our bacterial counts included *Synechococcus*. We filtered 20 l of 2 μm filtered seawater and spiked it with artificial ^{234}Th equilibrated with ^{238}U ; 10 ml of uranyl acetate solution (300 mg uranyl acetate in 1 N HCl) was used as the spike. Aliquots of 2 l were filtered periodically through 0.2 μm Nuclepore filters, and ^{234}Th activity was measured on the retentate as well as the filtrate, to avoid any uncertainties arising from adsorption of ^{234}Th on the walls. ^{234}Th activity in the 'solution' was on the order of 10 dpm ml^{-1} .

RESULTS AND DISCUSSION

The hydrographic data, the depth profiles of ^{234}Th concentrations in different particulate size fractions and the dissolved ^{234}Th concentrations are plotted in Figs. 1 & 2 for the 2 cruises. The ^{234}Th activities on the 0.1 to 1 μm fraction are corrected for filtering efficiency for bacteria. The data are given in Table 1 for the integrated amounts of carbon and ^{234}Th in the different particle-size reservoirs, for the 0 to 80 m water column for both the profiles.

Most of the ^{234}Th inventory (80% during both cruises) in seawater samples was in the $<0.1 \mu\text{m}$ ('dissolved') fraction (Table 1). This is consistent with previous findings on the distribution of ^{234}Th between the particulate and the dissolved phases (cf. Niven &

Moore 1988). The bacterial fraction was responsible for 32 and 40% of the total 'particulate' ^{234}Th inventory for the upper 80 m of the water column during October 1989 and July 1990 cruises, respectively.

Assuming that bacteria alone were responsible for ^{234}Th accumulation in the 0.1 to 1.0 μm fraction in the field samples their VCF was in the range of 10^6 to 10^7 (Table 2).

The ^{234}Th spike experiment (Fig. 3) supports the observation that the bacterial fraction had the capacity to accumulate ^{234}Th to high concentrations (VCF $\approx 7 \times 10^6$). Once again, this calculation assumes that bacteria alone were responsible for ^{234}Th accumulation and that fine detritus or protozoa which may have been present in the $<2 \mu\text{m}$ filtrate did not contribute significantly. While this assumption is probably not entirely correct, epifluorescence microscopy showed that bacteria were the dominant particulate component. We cannot rule out that particles which did not stain with DAPI were present and contributed to ^{234}Th adsorption. There are no previous measurements of VCF for natural assemblages of pelagic marine bacteria with which to compare our VCF values. However, the VCF values determined by us for the field and the spike samples are comparable to those determined for *Synechococcus* cultures (Fisher et al. 1987).

The concentration of ^{234}Th in seawater in the spike experiment was 2 orders of magnitude greater (ca 4.5 nCi m^{-3}) than in the field samples, yet the VCF in

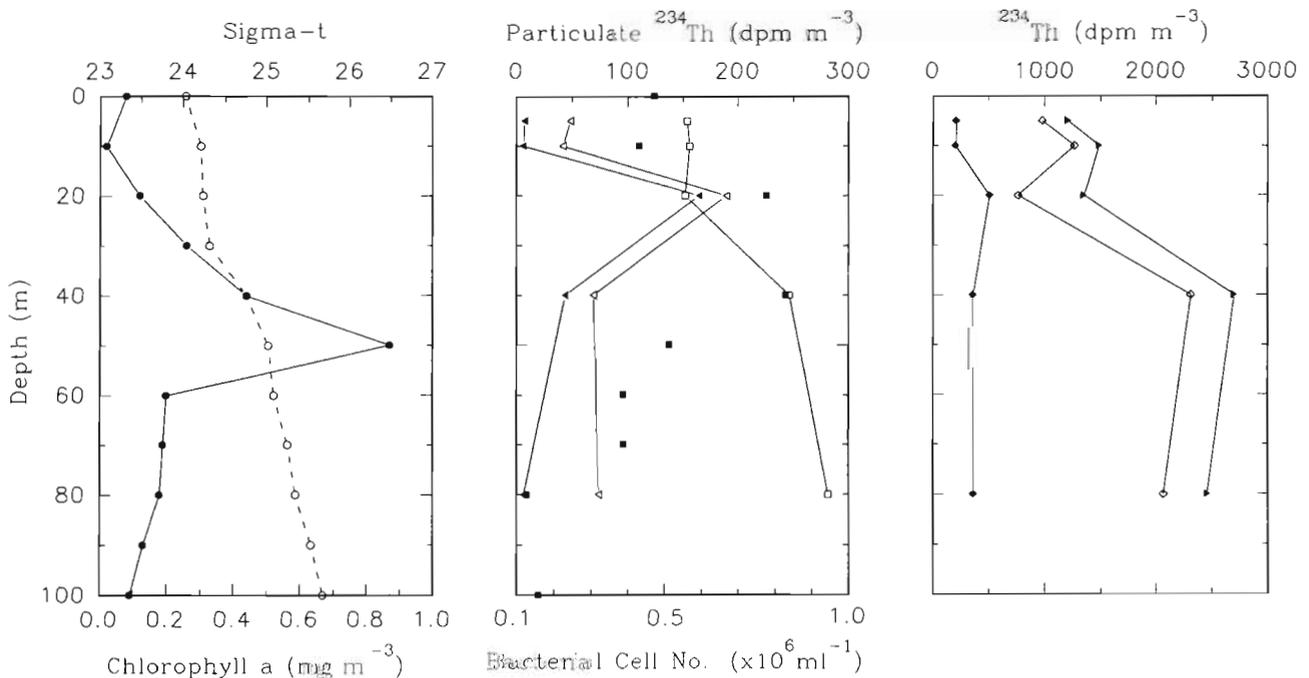


Fig. 1. Depth profiles of hydrographic parameters and ^{234}Th concentrations in the Southern California Bight at CALCOFI Stn 93.60 for October 1989 cruise. Sigma-t (\circ), chlorophyll a (\bullet); bacterial cell number (\blacksquare), particulate- ^{234}Th in 0.1–1 μm (\blacktriangleleft), 1–5 μm (\blacktriangle), $>5 \mu\text{m}$ (\square); and ^{234}Th concentrations in particulates (\blacklozenge), in dissolved phase (\diamond) and total ^{234}Th (\blacktriangleright)

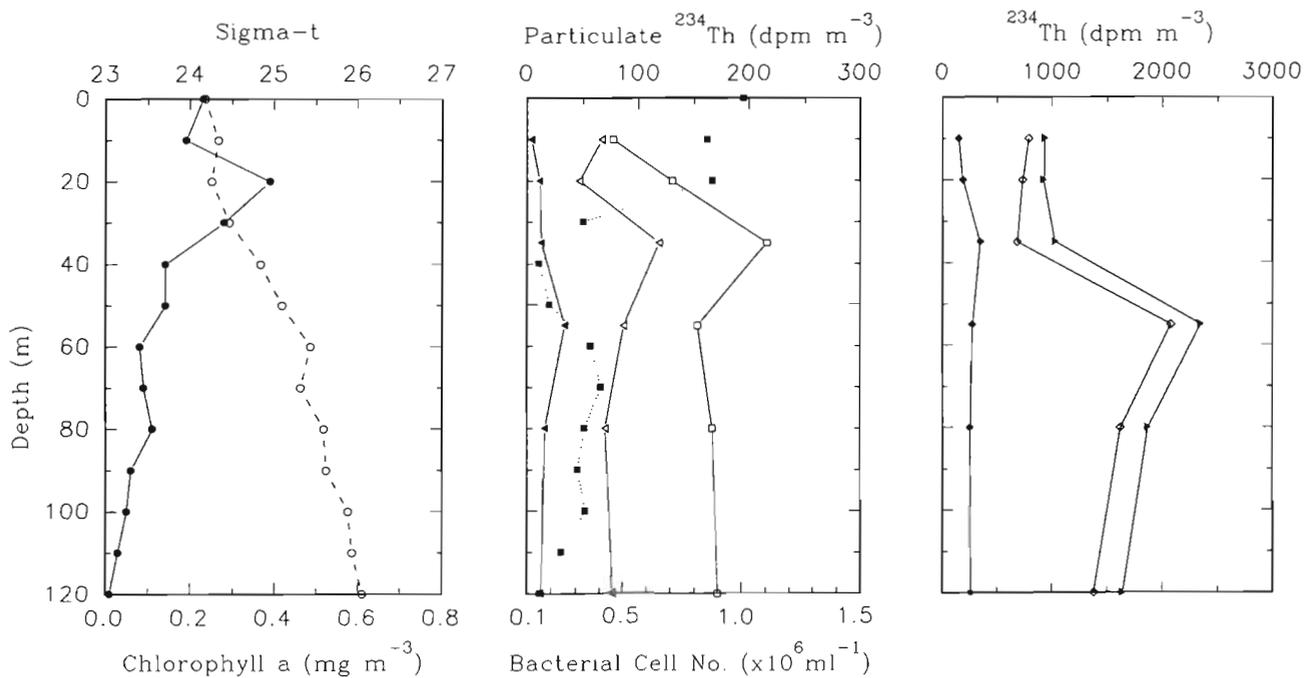


Fig. 2. As Fig. 1, for July 1990 cruise

the 2 cases was comparable. This indicates that the bacterial fraction had a much higher adsorptive capacity than is utilized in the field where the ambient 'dissolved' ^{234}Th concentration is much lower.

While our main goal was to determine the significance of bacteria in ^{234}Th scavenging we found it intriguing that the majority of particulate ^{234}Th was due to $>5\ \mu\text{m}$ fraction (55 and 53 % for the 2 cruises; Table 1), despite the expected low surface:volume ratio of this fraction relative to the bacterial fraction (Fisher et al. 1987). If the $>5\ \mu\text{m}$ fraction had much larger total particle volume than the bacterial fraction, this could have counterbalanced its low surface:volume ratio and would have explained its high ^{234}Th content. However, extensive previous work in our study area has shown that bacterial carbon, even in the euphotic zone, accounted for roughly one-half of the total POC (i.e. bacterial carbon was comparable to the sum of all other carbon pools; Cho & Azam 1988, 1990, Azam et al. 1992). Thus, even if all non-bacterial POC was assumed to be $>5\ \mu\text{m}$ this size-fraction would have very high $^{234}\text{Th}/\text{C}$ ratios for the bacterial fraction. Reasonable assumptions of the carbon content of DOC (1 to 2 mg C l^{-1} ; Druffel et al. 1989, Williams 1992, Martin & Fitzwater 1992) and its colloidal fraction (15 to 70 % of DOC; Baskaran et al. 1992) showed that the $^{234}\text{Th}/\text{C}$ ratio of the DOC pool was an order of magnitude lower than that of the bacterial and $>5\ \mu\text{m}$ fractions. Since we did not measure the ^{234}Th inventory of the colloidal fraction we could only set an upper limit

on the $^{234}\text{Th}/\text{C}$ ratio of the colloidal fraction by assuming that the entire <0.1 inventory of ^{234}Th was due to colloids. Even with this assumption, the $^{234}\text{Th}/\text{C}$ ratio of the colloidal fraction (0.56 to 5.2 and 0.4 to 3.8 nCi gC^{-1} from the 2 cruises; Table 1) was not high enough (compared to the values of 5.1 and 5.5 nCi gC^{-1} for the 0.1 to 1 μm and 7.7 and 6.3 nCi gC^{-1} for the $>5\ \mu\text{m}$ particle fractions) to meet the expectation based on the colloid pumping model.

Our results are difficult to reconcile with either the particle scavenging (Bacon et al. 1982) or the colloidal pumping model (Honeyman & Santschi 1989) since these models would require that the fine particles have a much higher ratio of $^{234}\text{Th}/\text{C}$ than the larger particles (unless the larger particles are exclusively composed of the smaller particles, for instance by coagulation). Also, it would not be expected that the $^{234}\text{Th}/\text{C}$ ratios for the DOC and colloidal carbon (COC) pools would be lower than all the 'particulate' carbon pools. The 'colloidal pumping' model would predict that the colloids would have the highest $^{234}\text{Th}/\text{C}$ ratio, except where the particulate phases were exclusively composed of coagulated colloids; in that situation the colloids and the 'particles' should have equal $^{234}\text{Th}/\text{C}$ ratios. Our results are consistent with those of Moran & Buessler (1992) in that the ^{234}Th activities of colloidal and 'small' particles (in their case, 0.2 to 53 μm) are comparable.

In order to explain our results we propose that the flow of ^{234}Th from the truly dissolved phase to colloidal

Table 1. ^{234}Th activity and carbon concentration factors for ^{234}Th in different size fractions of seawater samples, for 0 to 80 m water column. DOC: dissolved organic carbon; COC: colloidal carbon; POC: particulate organic carbon; BOC: bacterial organic carbon

Size fraction	October 1989 cruise			July 1990 cruise		
	nCi ^a m ⁻²	% of total	% of >0.1 μm	nCi ^a m ⁻²	% of total	% of >0.1 μm
Integrated ^{234}Th activity in 0 to 80 m column						
<0.1 μm	62.6	81.4	-	45.2	81.6	-
>0.1 μm	14.3	18.6	100	10.2	18.4	100
0.1–1 μm	4.6	6.0	32	4.2	7.5	41
1–5 μm	1.8	2.3	13	0.62	1.1	6.0
>5 μm	7.9	10.3	55	5.5	9.8	53
Total	76.9	-	-	55.4	-	-
Integrated mean $^{234}\text{Th}/\text{C}$ ratio^b (nCi gC⁻¹)						
Size fraction						
<0.1 μm		0.39–0.78			0.28–0.56	
COC ^c		0.56–5.2			0.40–3.8	
0.1–1 μm		5.1			5.5	
>5 μm		7.7			6.3	
Integrated carbon content (gC m⁻²)						
Carbon pool						
DOC ^d		80–160 ^d			80–160 ^d	
COC		(12–112) ^e			(12–112) ^e	
BOC		0.91 ^f			0.77 ^f	
POC (>5 μm)		1.03 ^g			0.87 ^g	

^a1 nCi = 37 Bq
^bBased on carbon pool sizes given in the lower portion of the table
^cMaximum estimates, based on the assumption that all <0.1 μm ^{234}Th was in the colloidal fraction
^dBased on an approximate DOC range of 1 to 2 gC m⁻³ (Druffel et al. 1989, Martin & Fitzwater 1992, Williams 1992). We assumed <0.1 μm C = DOC
^eColloidal mass was assumed to be 15 to 70 % of DOC (Baskaran et al. 1992)
^fThe carbon content of 0.1 to 1 μm fraction was assumed to be equal to BOC. This may be an underestimate since some non-bacterial POC is likely to be present in this size fraction; consequently, the calculated $^{234}\text{Th}/\text{C}$ ratios of 0.1 to 1 μm fraction may have been overestimated. The overestimation is probably well within a factor of 2 because the magnitude of BOC is generally comparable to all non-bacterial POC (Cho & Azam 1988, 1990)
^gTotal POC was calculated from the relationship: $1/\text{BOC} = 0.0205 + 2.0946/\text{POC}$ (Cho & Azam 1990). POC >5 μm was calculated as total POC minus BOC and therefore may be overestimated; consequently, the calculated $^{234}\text{Th}/\text{C}$ ratios of >5 μm fraction may have been underestimated. Our estimates of non-bacterial POC are comparable to estimates of total phytoplankton POC (1.01 and 0.9 gC m⁻² for October 1989 and July 1990, respectively; not shown) made on the basis of chl *a* measurements (Figs. 1 & 2) using the relationship: phytoplankton carbon = chl *a* \times 45. See Cho & Azam (1990) for a discussion of C : chl *a* ratios in the Bight

Table 2. Volume concentration factors for ^{234}Th for 0.1 to 1.0 μm particles

Depth (m)	Volume concentration factor ^a
October 1989	
5	4.2×10^6
10	2.8×10^6
20	1.7×10^7
40	1.3×10^6
80	1.0×10^7
July 1990	
10	4.0×10^6
20	2.7×10^6
35	3.4×10^6
55	5.7×10^6
80	4.8×10^6
120	1.4×10^7

^aBased on assumed mean bacteria volume of 4×10^{-14} ml in the study area (Cho 1988)

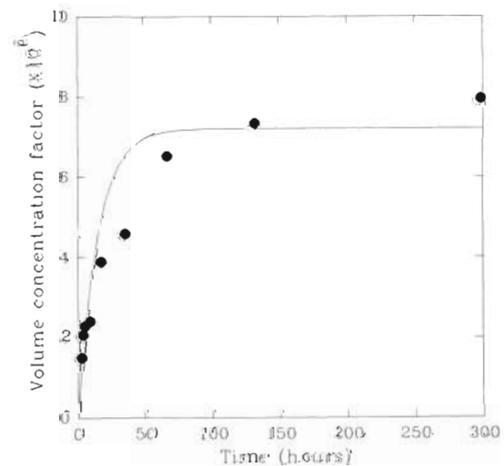


Fig. 3. Volume concentration factor (VCF) versus time for ^{234}Th adsorption by a bacterial fraction (<2 μm) of seawater. Mean adsorption time is of the order of 1 d

and particulate phases is 'unstructured' (Isaacs 1973). Our model is based on the premise of the colloidal pumping model that truly dissolved ^{234}Th first interacts mainly with colloids (Baskaran & Santschi 1992, Baskaran et al. 1992). However, we think it is critical to distinguish between 2 pools of ^{234}Th -reactive colloids, the 'disperse' colloids and the 'bound' colloids, both of which are able to scavenge ^{234}Th from truly dissolved phase. The colloidal pumping model considers only the disperse colloids while our model assumes that substantial amounts of colloids with high affinities for ^{234}Th occur bound to the surfaces of organisms and particles. Sorption of ^{234}Th to the bound ^{234}Th -reactive colloids should move ^{234}Th directly to particles of any size ('unstructured' flow). Colloidal pumping and unstructured flow would occur simultaneously, and the relative significances of the 2 mechanisms for transferring ^{234}Th to sinking particles will depend on relative abundances and affinities of ^{234}Th -reactive colloids in disperse and bound pools, which may, in turn, depend on the nutritional and physiological status of the microbial assemblages.

Bacteria and phytoplankton are generally covered with bound polysaccharides and proteoglycans which these organisms metabolically express on their surfaces and also release into seawater (Decho 1990). Bacteria represent the largest biotic surface in seawater (Williams 1981, Azam 1984, Cho & Azam 1988), therefore they may constitute the largest colloid-covered biological surface in the ocean (Azam et al. 1992). Scavenging of ^{234}Th by surface bound colloids of bacteria should move ^{234}Th from truly dissolved to fine particulate phase, bypassing the disperse colloidal phase. ^{234}Th could also move directly into suspended and sinking particulate phases. This is because bacteria themselves colonize marine particles of all sizes to high concentrations, 10^2 to 10^4 times greater than in seawater. Rapidly sinking aggregates ('marine snow') typically harbor 10^8 to 10^9 bacteria ml^{-1} (Alldredge & Gottschalk 1990, Smith et al. 1992) while suspended particles have bacterial concentrations on the order of 10^{10} ml^{-1} (Azam et al. 1992). Heavy colonization by bacteria would result in enrichment of particles of all sizes with respect to ^{234}Th . If bacteria on particles have higher ^{234}Th adsorption capacity (higher colloid content per bacterium and/or higher ^{234}Th affinity of bacterial surface colloids) than free bacteria then $^{234}\text{Th}/\text{C}$ of colonized particles could be enhanced by this direct scavenging mechanism. Bacteria colonizing marine aggregates generally secrete copious amounts of mucus which can form a layer covering the bacteria (Biddanda & Pomeroy 1988, Cochlan et al. 1991). Indeed, the mass of the mucus layer can exceed bacterial biomass (Hobbie & Lee 1980). Many different types of polysaccharides

are synthesized by microorganisms, hence there is potential for variability in the affinity of different polysaccharides for ^{234}Th . Large particles could therefore achieve high ^{234}Th due to colonization by and *in situ* growth of bacteria. In this situation, ^{234}Th movement to the large sinking particles would be direct and would bypass colloidal and fine particulate phases.

$^{234}\text{Th}/\text{C}$ of disperse colloidal phase roughly estimated in our study (Table 1) was actually lower than that of the bacterial and the >5 μm fractions. This could be because only a small fraction of the dispersed colloidal pool was surface reactive, but we normalized the ^{234}Th to the entire disperse colloidal pool. Also, the bound ^{234}Th -reactive colloids may have had higher affinity for ^{234}Th than the disperse colloids.

Trophic transfer of bacteria to protozoa is another possible mechanism which could increase $^{234}\text{Th}/\text{C}$ of larger particles. This would happen if respiratory losses of the ingested carbon were not balanced by excretion of ^{234}Th ingested along with the carbon. However, protozoan food vacuoles are acidic and exposure to this environment might desorb ^{234}Th from the particulate phase into the truly dissolved phase (Azam et al. 1992). The solubilized ^{234}Th would then be egested into seawater thus generating a futile cycle of adsorption-desorption without moving ^{234}Th up to larger particles (Azam et al. 1992). Pico- and nanophytoplankton can also be ingested by protozoa, and ^{234}Th associated with them might also be similarly remobilized into the dissolved phase. In fact, colloids can also be ingested by protozoa (Sherr 1988) and this could result in colloid-associated ^{234}Th as well being returned to the truly dissolved phase. If digestion by protozoa does actually return ^{234}Th to the truly dissolved phase then the entry of small organisms and particles into the microbial loop would be an inefficient way to transfer ^{234}Th to larger organisms or into their feces. However, aggregation of picoplankton and fine detritus could bypass this futile cycle and be important in transferring ^{234}Th up to the larger grazers and into their feces.

In conclusion, ^{234}Th movement from truly dissolved phase to the particulate phases probably occurs by the simultaneous operation of colloidal pumping and unstructured flow. We do not suggest that scavenging by colloids is unimportant in ^{234}Th dynamics. Rather, we emphasize that ^{234}Th scavenging by bound colloids should also be taken into account as an important variable which could fundamentally change the patterns of ^{234}Th fluxes in the ocean. The magnitude and the variability of unstructured flow should be tested in representative marine environments since it could have implications for the use of $^{234}\text{Th}/^{238}\text{U}$ disequilibrium in inferring particle fluxes in the ocean.

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